BITE PERFORMANCE AND FEEDING KINEMATICS IN LOGGERHEAD TURTLES (CARETTA CARETTA) WITHIN THE CONTEXT OF LONGLINE FISHERY INTERACTIONS

A Thesis

by

ALEJANDRA GUZMAN

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2008

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Christopher D. Marshall
Committee Members,	André M. Landry, Jr.
	Thomas J. DeWitt
Head of Department,	Thomas Lacher

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ABSTRACT

Bite Performance and Feeding Kinematics in Loggerhead Turtles (*Caretta caretta*) within the Context of Longline Fishery Interactions. (May 2008)

Alejandra Guzman, B.S., Trinity University

Chair of Advisory Committee: Dr. Christopher D. Marshall

Feeding biomechanics and foraging behavior are likely contributors to loggerhead sea turtle (*Caretta caretta*) bycatch in the pelagic longline fishery. To investigate these contributions, loggerhead bite performance was measured in several size classes of captive-reared juveniles, captive sub-adults and adults, as well as wild loggerheads. A kinematic study was conducted to investigate loggerhead interactions with modified longline hooks. Kinematic and behavioral variables were assessed in relation to five longline hooks to determine if loggerhead feeding behavior is modulated relative to hook type, size, and offset. The bite force study demonstrated that mean maximum post-hatchling bite force was 2.5N and mass was the best predictor of post-hatchling bite force. Mean maximum bite force of juveniles with mean straight carapace length (SCL) of 12, 31, 44, and 65 cm were 27, 152, 343, and 374 N, respectively. Sub-adult and adult mean maximum bite force was 575 N. Maximum bite force had a positive linear relationship with all head and body morphometrics ($P<0.001$). Carapace width was the best predictor of bite force throughout ontogeny. The kinematic study

demonstrated no differences between hook treatments in all kinematic variables analyzed. The results of this study suggest loggerhead feeding behavior may be stereotypical. Only 33% of all interactions resulted in “hooking” events. “Hooking” was lowest in 16 gage circle hooks with no offset and the 18 gage circle hooks with 10˚offset which may be indicative of a lower possibility of the turtle drowning. “Hooking” was highest in the 16 gage circle hooks with 10˚offset. The proportion of turtles “hooked” in the mouth was significantly greater than those “hooked” in the throat (P=0.001). Sixteen gage circle hooks with 10˚ offset had the highest percentage of throat “hooking”, and the 18 gage circle hooks without offset resulted in the lowest percentage of throat hooking. When interacting with J hooks with a 25˚ offset (9 gage), turtles mostly oriented their head away from the hook offset; however, when interacting with the 16 and 18 gage circle hooks with 10˚ offset, turtles mostly oriented their heads toward the hook offset. These data suggest that turtles may distinguish between small and large offsets, and may modulate their feeding behavior accordingly. Alternatively, turtles may be detecting hook size or hook shape. A more thorough characterization of loggerhead bite performance and feeding kinematics will be useful when developing or modifying longline fishery gear aimed at reducing loggerhead bycatch.

DEDICATION

To my family: Dad, Mom, Gabi, and Dani.

I love you.

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CHAPTER I

INTRODUCTION

Sea Turtle Origins and Population Status

Sea turtles originated in the Triassic and ancestral testudines possessed many of the characteristics of modern turtles. However, more derived clades in the Cretaceous evolved the remaining characteristics common to many Chelonians, such as the ability to retract the head into the shell. Major changes in the skull, jaw, and jaw musculature occurred during this time. Cretaceous testudines gave rise to the present cryptodire and pleurodire turtle radiations, which comprise all modern turtles (Carroll, 1988). Today, cryptodires are divided into three superfamilies, Testudinoidea (tortoises and most freshwater turtles), Trionychoidea (soft-shelled turtles), and Chelonioidea (marine turtles). There are currently seven species of marine turtles: olive ridley (*Lepidochelys olivacea*), Kemp's ridley (*L. kempii*), flatback (*Natator depressus*), hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), green (*Chelonia mydas*), and leatherback (*Dermochelys coriacea*). All hard-shelled turtles are in the family Chelonidae, and the leatherback belongs to the family Dermochelyidae. Six of the seven marine turtle species are currently considered endangered, and three species (leatherbacks, hawksbills, and Kemp's ridleys) are critically endangered (RLSPS, 1996; MTSG, 1996; Sarti Martinez, 2000; Seminoff, 2004). There is insufficient information to categorize the status of the flatback turtle that resides off Australia (RLSPS, 1996).

This thesis follows the style of *The Journal of Experimental Biology*.

Millions of sea turtles once roamed the oceans; however, now only several hundred thousands are left (Ripple, 1996). Hawksbill and leatherback populations have exhibited recent declines (Meylan, 1999; Spotila et al., 2000). Other sea turtle population trends demonstrate steady increases (Bjorndal et al., 1999b; Chaloupka and Limpus, 2001; Balazs and Chaloupka, 2004; Troëng and Rankin, 2005), although current populations are nowhere near what they were several decades ago (Ripple, 1996; Spotila, 2000).

Several anthropogenic affects have threatened all sea turtle populations. These include direct turtle and egg harvest, nesting habitat degradation and loss, and incidental take by several fisheries (Eckert, 1995; Spotila et al., 1996; Lutcavage et al., 1997; Spotila, 2000; Bugoni et al., 2001; Kamazaki et al., 2003; Limpus and Limpus, 2003; Stewart and Wyneken, 2004). Excessive commercial exploitation through a variety of fishery practices has caused population declines in many marine turtle species worldwide (Ross, 1995; Hays et al., 2003; Lewison et al., 2004; Lewison and Crowder, 2007). Loggerheads are the most common sea turtle species captured by the North American fishing industry (Hillestad et al., 1995). Recently, interactions between marine turtles and the longline fishing industry have become a growing concern.

Of the seven species of sea turtles, only loggerheads and leatherbacks are most common among longline bycatch constituents (Witzell, 1999; Kotas et al., 2002; Watson et al., 2004; Lewison et al., 2004; Pinedo and Polacheck, 2004; Gilman et al., 2006). Leatherbacks tend to become fouled in the gear whereas loggerheads are hooked (Witzell, 1999; Watson et al., 2004; Lewison et al., 2004; Gilman et al., 2006). The tendency for loggerheads to become hooked, rather than fouled, in the pelagic longline

fishery, suggests their feeding biomechanics (i.e. bite performance and feeding kinematics) may be involved in hooking interactions. Despite common knowledge that loggerheads are durophagous, and are capable biters, a systematic investigation of bite force, bite force development, or the kinematics of biting and feeding has not been conducted for loggerheads or any other marine turtle. Therefore, it is important to investigate these interactions and gain a complete understanding of loggerhead feeding biomechanics, particularly in the context of the longline fisheries. Such information may prove beneficial to the implementation of new fishing gear, fishing practices, or management strategies designed to decrease loggerhead bycatch. Therefore, the objectives of this study are two fold: 1) measure loggerhead bite performance throughout ontogeny and 2) examine loggerhead feeding kinematics when interacting with baited longline hooks. Investigations of loggerhead feeding biomechanics (through bite performance and feeding kinematics) will provide data that can be used to modify longline fishery gear, such as new hook designs, and potentially diminish sea turtle bycatch.

Loggerhead Natural History

Loggerhead turtles are one of the most thoroughly studied marine turtle species. Recent efforts have focused on understanding their early life history and biology (e.g., Carr, 1986; Dodd, 1988; Richardson and McGillivary, 1991; Burke et al., 1993; Bolten and Balazs, 1995; Godley et al., 1997; Bjorndal et al., 1997, 2000, 2003; Witherington, 2002; Bjorndal, 2003; Bolten, 2003a, 2003b; Hopkins-Murphy et al., 2003; Kamezaki,

2003; Steward and Wyneken, 2004; Parker et al., 2005; Sasso and Epperly, 2007). Loggerhead hatchlings leave their natal beaches and lead an oceanic existence for up to 12 years (Figure 1) (Bolten and Balazs, 1995; Bjorndal et al., 2000). During this period, they spend approximately seventy-five percent of their time in the top 5 m of the surface, tend to swim with prevailing currents, and associate with sargassum rafts for food and protection (Carr, 1986, 1987; Bolten and Balazs, 1995; Witherington, 2002; Spotila, 2004; Parker et al., 2005). Juvenile loggerheads are considered omnivorous and feed on a wide variety of food items within the sargassum community including larval and small invertebrates (*Planes, Lepas, Latreutes*), pieces of vascular plants (*Syringodium, Cymodocea, Thalassia, Zostera*), algae (*Ascophyllum, Fucus, Sargassum, Ulotrhrix, Ulva, Urosporta*), insects, gelatinous zooplankton (*Carinaria, Pelagia, Pyrosoma, Velella*), and decapod crustaceans (Richardson and McGillivary, 1991; Burke et al., 1993; Ernst et al., 1994; Bjorndal, 1997; Dodd, 1988; Witherington, 2002; Spotila, 2004; Parker et al., 2005). Loggerheads may grow up to 60 cm in straight carapace length (SCL) during this life stage (Bjorndal et al., 2000). Juveniles in this oceanic phase of their natural history are susceptible to interactions with pelagic longline fisheries (Hillestad et al., 1995; Ross, 1995; Witzell, 1999; Lewison et al., 2004; Carranza et al., 2006; Sasso and Epperly, 2007).

Loggerheads undergo an ontogenetic shift and recruit to shallow neritic environments along the continental coast late in their oceanic juvenile life stage (approximately 42-58 cm SCL) (Figure 1) (Carr, 1986; Bjorndal et al., 2000, 2003). They concentrate their foraging efforts on benthic prey; however, smaller individuals

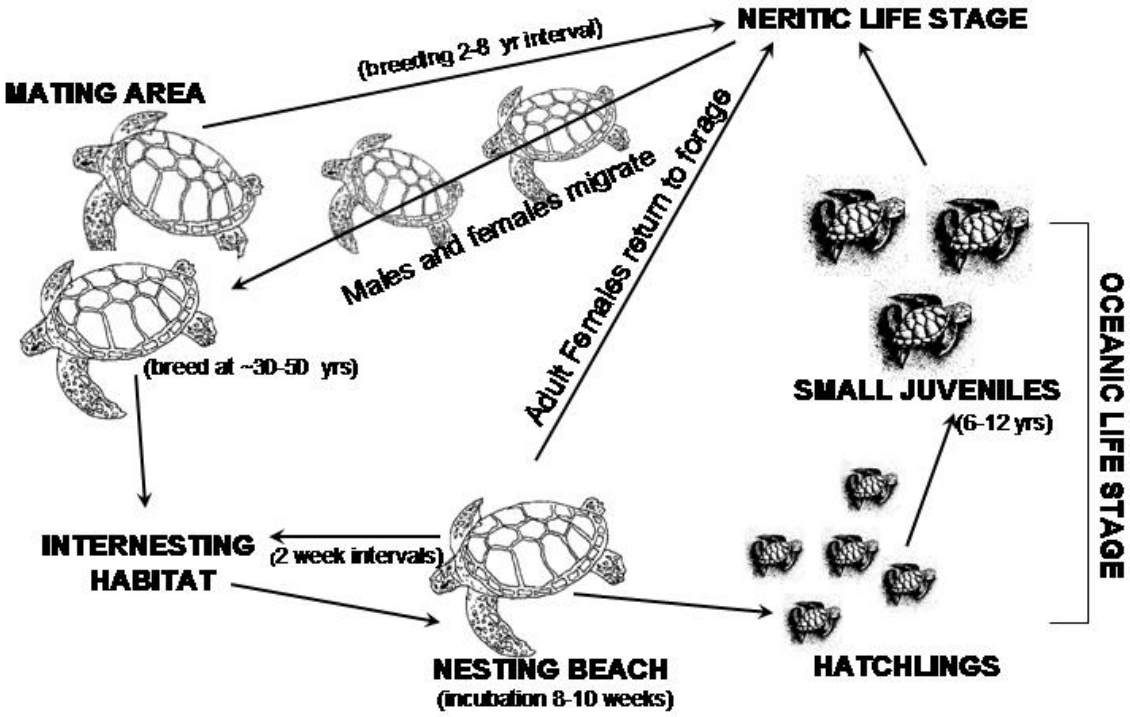

Figure 1. Loggerhead Life Cycle. The path of a loggerhead sea turtle from the hatchling phase until maturity is reached, reproduction occurs, and eggs are laid on the beach.

still forage throughout the water column (Mortimer, 1995; Bjorndal, 1997, 2003; Spotila, 2004; Revelles et al., 2007). Loggerheads ingest a wide variety of invertebrates with hard exoskeletons (Ernst et al., 1994; Bjorndal, 1997; Bjorndal, 2003) and are considered durophagous. Their carnivorous diet consists mainly of sessile or slow moving, bottom-dwelling invertebrates including various species of crabs (e.g., *Hepatus, Planes, Portunus, Libinia, Limulus, Callinectes, Cancer, Pagurus, Persephona, Ovalipes*), gastropod mollusks (*Janthina, Neverita, Litiopa, Diacria, Pterotrachea, Mytilus, Busycon, Strombus*), bivalves (*Anadara, Pinna, Solen, Amusium, Mytilus, Tridacna*), and barnacles (*Lepas*). Many pelagic, soft prey, if available, are also eaten, including squid (*Loligo*), sea anenomes (*Stichodactyla*), sea pens (*Virgularia*), sea horses (*Hippocampus*), gelatinous species (*Velella, Carinaria, Pelagia, Pyrosoma, Cotylorhiza*), and fish species (*Brevoortia, Ceratoscopelus, Cynoscion, Diodon, Micropogonias, Morone, Pomotomus, Scomber*) (Lutcavage and Musick, 1985; Dodd, 1988; Burke et al., 1993; Plotkin et al., 1993; Ernst et al., 1994; Limpus et al., 1994; Bjorndal, 1997; Godley, 1997; Tomas et al., 2001; Bjorndal, 2003; Bolten, 2003b; Hopkins-Murphy et al., 2003; Spotila, 2004; Parker et al., 2005; Revelles et al., 2007; Seney and Musick, 2007). Loggerhead diet and foraging ecology appear to be dictated by location and availability of prey (Bjorndal, 2003; Seney and Musick, 2007). Larger juveniles and older individuals (> 60 cm) rarely interact with the longline fishery as a result of this ontogenetic shift into neritic, benthic environments.

Bite Performance

Ontogenetic changes in diet are often accompanied by biomechanical shifts in skull architecture and jaw musculature, and as a result bite performance (e.g., Stoner, 1980; Eggold and Motta, 1992; Luczkovich et al., 1995; Wainwright and Richard, 1995; Hernandez and Motta, 1997; Binder and Van Valkenburgh, 2000; Monterio et al., 2005; Herrel and O'Reilly, 2006). The feeding apparatus of loggerheads change dramatically throughout their ontogeny (Kamezaki, 2003), and it is likely that morphological shifts occur during ontogenetic shifts in diet and habitat, as found in other vertebrates. Adult coastal loggerheads are durophagous, and that their large head and powerful jaws are adaptations for crushing hard-shelled prey (Ernst et al., 1994; Mortimer, 1995; Kamezaki, 2003). Descriptive accounts support this claim, but no specific data are available. Compared to green and hawksbill sea turtles (Ernst et al., 1994**;** Kamezaki, 2003), the heads of adult loggerheads are short and wide, hence the name "loggerhead." Correspondingly, their jaws are also shorter. A larger head and short, robust jaws are adaptations that would increase bite force through an increased mechanical advantage (due to the decreased out-lever) and an increase of the in-force of the lever system (increase in the mass of the adductor mandibulae). Because all turtle skulls are constrained by the anapsid condition (lack of temporal fenestrations), an increase in head width would be one of the few mechanisms, in addition to shortening the jaw, to increase bite force considerably. However, biomechanical analysis of the jaw joint remains to be conducted.

Although data are lacking to test the perception that loggerheads are capable of powerful bites, bite performance studies have been conducted on a variety of vertebrates including: lizards (Herrel et al., 1999; Herrel et al., 2001a; Herrel et al., 2001b; Verwaijen et al., 2002; Herrel and O'Reilly 2006), freshwater turtles (Herrel et al., 2002; Herrel and O'Reilly, 2006), alligators (Erickson et al., 2003), sharks (Snodgrass and Gilbert, 1967; Huber et al., 2005), finches (Herrel et al., 2005; Vanhooydonck et al., 2005), bats (Dumont and Herrel, 2003; Dumont et al., 2005), hyenas (Binder and Van Valkenburgh, 2000), primates (Dechow and Carlson, 1983) and other mammals (Kiltie, 1982; Thomason, 1991; Strom and Holm 1992; Thompson, 2003; Wroe et al., 2005). However, only a few studies have examined bite force across ontogeny (Binder and Van Valkenburgh, 2000; Thompson et al., 2003; Erickson et al., 2003; Herrel and Gibb, 2005; Herrel and O'Reilly, 2006). Measuring bite force is a non-invasive method that can provide insight into an organism's prey spectrum based on prey size and hardness, handling time, energetic costs, and prey capture success (Aguirre et al., 2002; Binder and Van Valkenburgh, 2000; Herrel and Gibb, 2005; Erickson et al., 2006). Increased bite force may provide ecological advantages such as resource partitioning and niche differentiation which could lead to decreased competition, an increase in the prey spectrum to more energy-rich items, and coexistence of several species within the same habitat (Kiltie, 1982; Herrel et al., 1999; Binder and Van Valkenburgh, 2000; Herrel et al., 2001b; Herrel et al., 2002; Dumont et al., 2005; Wroe et al., 2005).

Van der Klaauw (1948) termed the study of the relationship between an organism's morphology and its environment, ecological morphology (also termed

"ecomorphology"). Numerous studies have examined this relationship (e.g., Alexander, 1988; Barel et al., 1989; Bock, 1990; Losos 1990; Norton, 1991; Wainwright, 1991; Motta and Kotrschal, 1992). Behavioral performance testing provides the link between morphology and ecology (Wainwright and Reilly, 1994) and, ultimately, fitness (Arnold, 1983). There are ample data for lizards and turtles that suggest a strong link between morphology, bite force, and diet during growth (Herrel and O'Reilly, 2006). Several studies (Herrel et al., 2002; Herrel and Gibb, 2006; Herrel and O'Reilley, 2006) have measured bite performance in numerous freshwater turtle species, but ontogenetic bite performance information on any turtle species is absent from the literature. Bite force patterns among freshwater species demonstrate that omnivorous species have a lower maximum bite force relative to similar sized durophagous and carnivorous species (Herrel et al., 2002). Extrapolating these data to loggerheads, once body size is accounted for, suggests that loggerhead bite force should be relatively high. Since oceanic juveniles are omnivorous, it is expected that bite force in these size classes would be similar to bite force observed in similar sized omnivorous freshwater turtles. Bite force could be expected to increase rapidly, relative to body size, once sub-adults and adults recruit to coastal habitats.

Feeding Kinematics

There are three modes of feeding among aquatic vertebrates: 1) inertial suction - expansion of the buccal cavity (through depression of the hyoid apparatus) during mouth opening that causes a negative change in buccal pressure forcing prey into the mouth; 2)

ram feeding - ingestion of prey where the predator lunges forward to engulf prey without ever using the jaws; and 3) jaw prehension or biting - closing the mouth around prey so it is trapped within the jaws using little to no hyoid movement (Lauder, 1985; Norton and Brainerd, 1993; Deban and Wake, 2000; Wilga et al., 2007). Suction feeding is the ancestral mode of prey capture in ray-finned fishes (Lauder, 1985). Numerous studies have examined feeding kinematics in aquatic feeding vertebrates such as elasmobranches (e.g., Dean et al., 2007; Wilga et al., 2007), ray-finned fishes (e.g., Gibb, 1995, 1996, 1997; Wainwright, 1996; Wintzer and Motta, 2005; Beck and Turingan, 2007; Wainwright et al., 2007), salamanders (Lauder and Shaffer, 1985; Shaffer and Lauder, 1985; Reilly and Lauder, 1988; Gillis and Lauder 1994; Reilly, 1995; Deban and Wake, 2000), frogs (Dean, 2003), turtles (Bels and Renous, 1992; Lauder and Prendergast, 1992; Van Damme and Aerts, 1997; Summers et al., 1998), and marine mammals (Werth, 2000a, 2000b; Bloodworth and Marshall, 2005; Marshall et al., 1998, 2000, 2003). Suction feeding is characterized by a large hyoid depression and buccal expansion when feeding (Lauder, 1985; Lauder and Prendergast, 1992; Reilly and Lauder, 1992; Werth, 2000a, 2000b). The kinematic profile of suction feeding in most aquatic vertebrates, with respect to timing and head movement variables (jaw opening, hyoid depression, mouth closing), is fairly conserved which is thought to be a result of strong selection pressures of the aquatic environment: water is dense and viscous (Lauder, 1985; Van Damme and Aerts, 1997). Although some aquatic feeding appears stereotypical both within and between species (Lauder, 1985; Lauder and Shaffer, 1985; Shaffer and Lauder, 1989; Reilly, 1995) and throughout ontogeny (Reilly, 1995), it has

been suggested that feeding kinematics may be modulated based on prey type (Lauder and Prendergast, 1992) and environment (Summers et al., 1998).

Aquatic feeding kinematics among freshwater turtle species is predominately ram feeding (Lauder and Prendergast, 1992; Bels and Renous, 1992; Summers et al., 1998), although one species, *Chelodina*, exhibited a combination of compensatory and inertial suction during feeding (Van Damme and Aerts, 1997). Compensatory suction often occurs during ram feeding and differs from inertial suction in that prey is not drawn into the mouth by pressure gradients alone. During ram feeding, compensatory suction merely reduces or eliminates the potential pressure wave produced ahead of the predator during a strike. Since aquatic feeding in freshwater and terrestrial turtles seems conserved, it is likely that loggerhead sea turtles will also exhibit similar ram feeding kinematics for prey capture. Furthermore, it is possible that loggerheads may modulate their feeding based on data from Summers et al. (1997) that demonstrated freshwater turtles will modulate their feeding behavior based on prey type.

Fishery Interactions

Historically, sea turtles have been incidentally caught by gill nets, drift nets, trawls, longlines, and other fishing methods (Hillestad et al., 1995; Gardner and Nicols, 2001; Bolten, 2003a). Interactions between marine turtles and the longline fishing industry have become a growing concern. Global pelagic longline fishing methods target various species of tuna (*Thunnus obesus, T. albacares, T. alalunga*), billfish (*Xiphias gladius, Tetrapturus audax*), shark (*Carcharhinus longimanus, C. falciformis,*

Galeocerdo cuvier, Prionace glauca, Alopias superciliosus, Isurus oxyrinchus), and numerous other commercially valuable species (Beverly et al., 2003). Unfortunately, there are thousands of sea turtles taken as bycatch in this fishery (Nishemura and Nakahigashi, 1990; Lewison et al., 2004). Lewison et al. (2004) estimated up to 14 loggerheads were caught incidentally for every 1,000 longline hooks fished. By extrapolating these data, they estimate over 200,000 loggerheads were caught globally in the longline fishing industry during the year 2000 (Lewison et al., 2004). Drowning is one of the leading causes of sea turtle death since the turtles get hooked on longline gear and cannot reach the surface to breathe.

Loggerheads readily interact with and swallow baited longline hooks (Witzell, 1999; NMFS, 2001; Swimmer, 2002). Loggerhead populations are under intense pressures resulting from bycatch in the longline fishing industry, which is likely responsible for the decrease in nesting females in the Pacific over the last 40 years (Spotila et al., 2000; Lewison et al., 2004). Such intense pressures are a threat to this species' survival (Hillestead et al., 1995; Ross, 1995; Deflorio et al., 2005, Carranza et al., 2006; Lewison and Crowder, 2007).

Although fishing gear and methods vary greatly upon region, squid baited 9/0 J-hooks with 20-25˚ offset are the predominant hook traditionally used in the pelagic longline fishing industry (Watson et al., 2005). Loggerheads are more likely to swallow J-hooks than circle hooks (Bolten et al., 2002, Watson et al., 2003, 2005; Bolten and Bjorndal, 2005). Some studies suggest changing hook type (specifically to circle hooks), size, offset and bait can significantly decrease turtle-longline interactions (Bolten et al.,

2002; Garrison, 2003; Watson et al., 2003, 2004a, 2004b, 2005; Bolten and Bjorndal, 2005) without significantly affecting some targeted fish catch (Garrison, 2003; Watson et al., 2003, 2004a, 2004b, 2005). However, certain longline hooks were found to decrease catch per unit effort (CPUE) of targeted tuna species (Watson et al., 2004a, 2004b, 2005) and not reduce turtle-longline interactions in all situations (Bolten et al., 2002). The interactions between loggerheads and the longline fishing industry may be a result of this species' foraging behavior during its juvenile oceanic stage.

Objectives and Hypotheses

The objective of this study is to characterize the feeding biomechanics of loggerheads by measuring the ontogeny of bite force performance and conducting a kinematic study of their feeding behavior. The ontogeny of loggerhead bite force was measured across several classes of captive-reared, rehabilitating, and wild loggerheads (post-hatchlings, 6-10 cm SCL; juveniles, 12, 30, 45, and 60 cm mean SCL; sub-adults and adults, $\geq$ 60 cm SCL). I hypothesized the following: 1) bite force increases with age and size, 2) rate of bite force development is greatest in post-hatchlings ($\leq$ 6 months of age), 3) bite force measured in juvenile turtles is greater than 50% of bite force observed in sub-adult and adult individuals, 4) wild turtles have significantly larger bite force compared to that of similar sized captive turtles, and 5) bite force throughout ontogeny follows a sigmoidal pattern with large increases in bite force early in development until a plateau is reached in sub-adults and adults.

The body or head morphometric that best predicted bite force in post-hatchlings and throughout loggerhead ontogeny was determined. It was hypothesized that all body and head morphometrics are positively correlated with bite force, while head width best predicts bite force.

Loggerhead feeding kinematics was also characterized. It was hypothesized that the feeding kinematic profile exhibited by loggerheads is also conserved, compared to that of aquatic feeding freshwater turtles, and that prey capture is accomplished primarily by a ram feeding mode.

Lastly, ten kinematics variables (related to timing, distance, and angles) and five behavioral variables (proportion of “hooking”, "hooking” location, and head orientation) were analyzed to determine whether loggerheads modulate their feeding behavior when feeding on different squid baited longline hooks. I hypothesized the following: 1) loggerheads modulate their behavior relative to hook type, hook size and hook offset angle, 2) larger hooks result in fewer “hooked” incidents and “hooked” in the throat interactions due to the size of the hook, 3) smaller hooks, J and 16 circle hooks, result in more “hooked” and “hooked” in the throat events, 4) loggerheads feeding from hooks without offset (0˚) result in the most “hooked” and throat interactions, 5) loggerheads feeding from hooks with offset will interact with the side of the turtle’s mouth in the mandible area, and 6) loggerheads distinguish between large (25˚) and small hook offsets (0˚-10˚). It is predicted that 18 gage circle hooks with the largest offset (10˚) are the most effective in decreasing harmful (“hooked” in the throat) turtle-longline fishing gear interactions. These investigations of simulated loggerhead-longline fishery

interactions will provide data that can be used to develop longline fishery gear that may potentially reduce loggerhead bycatch.

CHAPTER II

ONTOGENY OF BITE PERFORMANCE

Introduction

Ontogenetic changes in habitat and diet, typical of loggerheads, are likely associated with changes in feeding and bite performance coupled with developmental changes in the skull structure and jaw musculature (Kamezaki, 2003). Such ontogenetic shifts in diet and corresponding shifts in morphology and performance has been observed in ray-finned fish (Hernandez and Motta, 1997; Wainwright and Richard, 1995; Hjelm et al., 2000, 2003; Svanbäck and Eklöv, 2002), lizards (Ballinger et al., 1977; Capel-Williams and Pratten, 1978; DeMarco et al., 1985; Paulissen, 1987; Herrel et al., 1999b; Herrel and O'Reilly, 2006), freshwater turtles (Herrel et al., 2002; Herrel and O'Reilly, 2006), and hyenas (Binder and Van Valkenburgh, 2000).

Adult coastal loggerheads possess relatively large heads and powerful jaws that are presumably adapted for crushing hard-shelled prey (Ernst et al., 1994; Mortimer, 1995; Kamezaki, 2003). Compared to green (*Chelonia mydas)* and hawksbill (*Eretmochelys imbricate)* sea turtles (Ernst et al., 1994; Kamezaki, 2003), the heads of adult loggerheads are short and wide, hence the name "loggerhead." Correspondingly, their jaws are also shorter. A larger head and short, robust jaws are adaptations that should increase bite force through an increase in the in-force of the lever system (increase in the mass of the adductor mandibulae) and an increased mechanical advantage (due to the decreased out-lever). Because all turtle skulls are constrained by the anapsid condition (lack of temporal fenestrations), the only way for loggerheads to

increase bite force is to increase the size of their head, and therefore increase in-force of the jaw depressors, or increase the mechanical advantage of the jaw lever. The loggerhead's wide head, robust jaw plates, strong mandible musculature, and presumable elevated bite performance are likely adaptations for durophagy, a foraging behavior that may allow loggerheads to access prey not available to other turtles or predators and render this species vulnerable to longline fishery gear. Increased bite performance associated with a durophagous diet would only render this species vulnerable to the longline fishery if this bite performance increase occurred in pelagic juveniles that typically interact with the fishery (40-60 cm SCL). However, no data are available that characterize loggerhead bite performance.

Therefore, the objectives of this study were to 1) measure bite performance in loggerheads throughout ontogeny, 2) determine which body or head morphometric best predicted bite force in post-hatchlings and throughout ontogeny, 3) provide bite force data that helps to broaden our understanding of loggerhead natural history, and 4) compare loggerhead bite force to bite performance from other vertebrates. Bite force was expected to increase with size and we predicted that the best predictor of bite force in post-hatchlings would be body morphometrics, whereas the best predictor of bite force throughout the observed loggerhead ontogeny would be head morphometrics, as found in other reptiles, due to the location of the jaw musculature. We predicted that bite force would follow a sigmoidal trend throughout ontogeny and would reach a plateau in the largest individuals. This data can be used to determine if there is a clear distinction, with respect to an increase in bite performance, associated with ontogenetic

changes in habitat and diet, and if this rapid bite force increase occurs in loggerhead size classes that typically interact with the longline fishery.

Materials and Methods

Subjects

Captive-reared loggerhead turtles held at the NOAA Fisheries Service Galveston Laboratory sea turtle facility (Galveston, TX, USA) were used in this study. Loggerheads younger than 2 years ($\leq$ 35 cm SCL) were fed pellet food twice daily while older juveniles (> 35 cm SCL) were fed squid twice a week. All captive turtles at this facility are released into the wild near age three (approximately 40-60 cm SCL, the most common bycatch size in the longline fishery). Husbandry and research activities on all captive-reared loggerheads at this facility are conducted under Florida Wildlife Conservation Commission permit TP#015. All procedures were approved by the Texas A&M University Institution Animal Care and Use Committee (animal use protocol # 2005-204).

Bite force measurements were collected from individual post-hatchlings (6-10 cm SCL), and from each of the four size classes of captive-reared juvenile loggerheads available at the holding facility: 12, 31, 44, and 63 cm mean SCL. Post-hatchlings used in this study were measured each month for 4 months. Post-hatchlings were 2 months old at the beginning of the 4-month study. For reasons outside the scope of this study, growth was accelerated in the 63 cm SCL size class of captive-reared juveniles (n=24), which explains the differential in size between the 44 and 63 cm SCL individuals.

Larger sub-adult and adult captive turtles were available from Camp Archelon (Bahia de los Angeles, Mexico) (BLA), Sea Turtle Inc. (South Padre Island, TX, USA) (STI), and Moody Gardens Aquarium (Galveston, TX, USA) (MGA). Bite force from free-ranging turtles was collected opportunistically through Sea Turtle Inc., St. Lucie power plant (Port St. Lucie, FL, USA) (PSL), hook and line captures, incidental captures, oil platform removals, and live strandings off the Texas gulf coast near Galveston (GAL). All wild turtles encountered in Galveston waters were temporarily housed at the NOAA Fisheries Service Galveston laboratory sea turtle facility and later released. All turtles were isolated and held in similar tank conditions (i.e. air and water temperature). Bite force was collected between February 2006 until August 2007 from a total of 154 loggerheads.

Morphometrics

Prior to bite performance trials, the following body and head morphometrics were obtained from each turtle (following Wyneken, 2001): straight carapace length, straight carapace width (CW), mass, head width (HW), head height (HH), and head length (HL). Straight carapace length was the straight-line measurement from the anterior-most point one the midline of the nuchal scute to the posterior-most tip of the last marginal scute. Straight carapace width was the straight-line measurement at the widest part of the carapace. Head width was measured at the widest part of the head. Head height was measured at the highest part of the skull just posterior to the orbits.

Head length was measured from the anterior-most part of the upper jaw to the posterior-most bone of the skull, also known as the supraoccipital crest.

Bite Force Measurements

Bite performance was measured with a bite meter (modified for a loggerhead mouth) consisting of adjustable bite plates and a piezo-electric force transducer (low load sensitivity: $\pm$ 500 N; Kistler FSH 9203; high load sensitivity: ~ $\pm$ 5000 N; Kistler FSH 9312A, Amherst, NY, USA) (Figure 2). A similar bite force apparatus was originally developed to measure bite force in lizards (Herrel et al., 2001b; Aguirre et al., 2002). Once bitten upon, the upper plate transfers the force to the force transducer. Signals from the transducer were amplified by a handheld charge amplifier (Kistler FSH 5995, Amherst, NY, USA) and recorded. The responses of these force transducers are linear across their entire range and at a wide range of temperatures. The accuracy of the bite meter output was independently calibrated by hanging a series of weights from the end of the bite force plates, and output was plotted to insure linearity. Raw bite force values were adjusted for mechanical advantage (ratio of output force to the input force) of the apparatus. Anterior bite force was measured at the tips of the maxillary and dentary bones of the jaw. The area of the biting surface was 63 mm^2, therefore all bite force values presented are in N/mm^2. Using the location of the bite point on the bite meter surface bars and the commissure of the turtle's mouth, gape angle, at the time of bite, was determined using Image J software (Bethesda, MD, USA). This was used to standardize gape angle throughout the study.

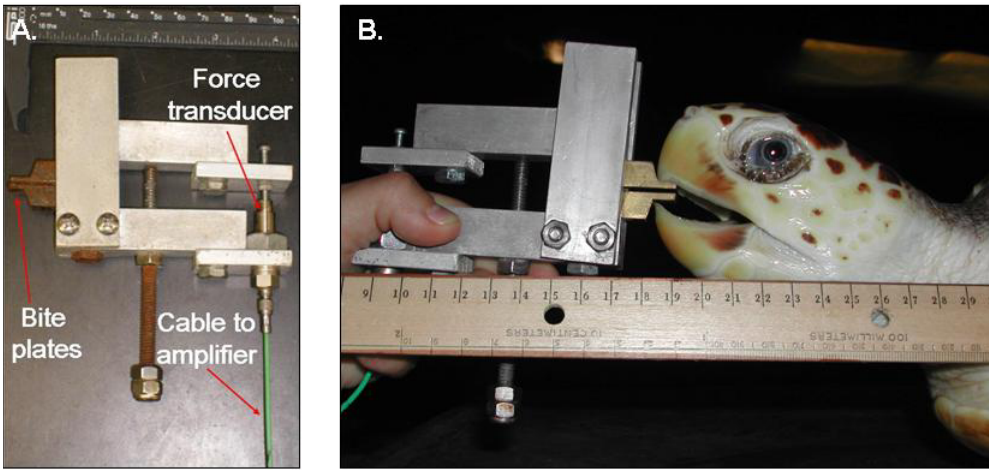

Figure 2. Bite Force Apparatus. A. Bite meter. A cantilevered upper bite force leverages forces to the transducer through an adjustable fulcrum and bite plates. B. Bite force apparatus and bite force plates modified for loggerhead sea turtles. Bite force being measured from a loggerhead from the 31 cm size class.

Three bite force measurements were collected per individual from post-hatchling turtles less than 6 months old (6-10 cm SCL; n=28). Post-hatchling bite force was collected monthly from each turtle once a day over multiple days for 4 months to correlate size, development, and rate of bite force over time in this longitudinal study to account for individual variability. Five bite force data points were collected from all juvenile captive-reared individuals within each size class over 2 or more days with at least 15 minutes between measurements. All bite force values obtained from each turtle were measured within one week. At least three bite force measurements were taken from captive and wild sub-adult and adult turtles, and analyzed to compare bite force between wild and captive loggerheads. Rate of bite performance increase was then further examined too distinguish when bite performance increases were highest and if this increase could be correlated with the ontogenetic shifts in diet and habitat typical of loggerheads. Bite force measurements in all turtles were taken prior to daily feeding so that motivation to bite would be high. Bite force data were only evaluated in healthy individuals that were motivated to bite. The maximal value obtained during measurements was considered to be the maximum bite force for that individual.

Statistical Analyses

Data were tested for normality and variance homogeneity using the Kolmogorov-Smirnov and Levene tests, respectively. One way analysis of variance (ANOVA) tests were performed to determine if bite force differed between months in the post-hatchling study, and in each size class throughout the observed ontogeny. Scheffé's *post-hoc* tests

were used to determine where differences in bite force occurred between months in the post-hatchling study, among the size classes throughout the observed ontogeny, and between wild and captive sub-adult and adult individuals. Morphological and bite performance variables were logarithmically transformed (log_{10}) to meet all normality and heterogeneity assumptions. Bite force was regressed against body and head morphometrics to investigate correlations between morphology and performance. To determine which morphological measure had the strongest correlation with bite force, a stepwise multiple linear regression was performed with bite force as the dependant variable and the body and head morphometric measures as the independent variables. Bite force data for all turtles were then regressed against SCL to determine what type of curve estimation equation best fit the bite performance data throughout ontogeny.

Regression analysis was used to examine bite performance trends in 132 species from different vertebrate groups (following Huber et al., 2005). Log transformed bite force was regressed against log transformed mass. The unstandardized residuals were then used for further analyses. Bite force residuals were used to compare loggerhead bite performance among other vertebrates. ANOVA was used to compare bite force residuals between vertebrate groups (i.e. mammals, fish, birds, and reptiles) and Scheffé *post-hoc* tests determined if any pair-wise differences were present (following Huber et al., 2005). All statistical analyses were performed using SPSS (ver. 14.0).

Results

Captive-Reared Post-Hatchlings and Juveniles

Mean maximum post-hatchling bite force increased significantly each month ($P<0.001$) except between the last 2 months of the post-hatchling study (month 5 and 6) (Figure 3). Mean maximum bite force in post-hatchlings (6-10 cm SCL) was 2.5 N with mean monthly increases of 0.8 N except for the last month when it was only 0.3 N. Post-hatchling body and head morphometrics increased slightly each month during the 4-month study. Mean monthly somatic and cranial growth throughout the post-hatchling study was 0.93 cm for SCL, 0.73 cm for CW, 2.0 mm for HW, 2.5 mm for HH, 3.0 mm for HL, and 22 g for mass. In general, bite force increased with age and size; there was a positive linear relationship between all body and head morphometrics and maximum bite force ($P<0.001$). Multiple linear regression demonstrated that mass (M_b) was the best predictor of post-hatchling bite force (F_b) (($LogF_b$) = -1.387 + 0.938 (($LogM_b$); Adj. R^2 = 0.650; Figure 4). All post-hatchling morphometrics and bite force data are summarized in Table 1. Mean maximum bite force increased in each juvenile size group. Mean maximum bite force of 12, 31, 44, and 63 cm mean SCL loggerheads was 27, 152, and 343, and 374 N, respectively. Statistical differences in bite performance were observed among all size classes ($P<0.001$) except between the 6 and 12 cm SCL and 44 and 63 cm SCL size classes (Figure 5). The smallest increase in bite force among size classes was observed between the 6 and 12 cm SCL juveniles while the largest increase was observed between the 31 and 44 cm SCL groups. Bite force increased 191 N (two times) between the 2 latter size classes. Bite force only increased 31 N between these two size

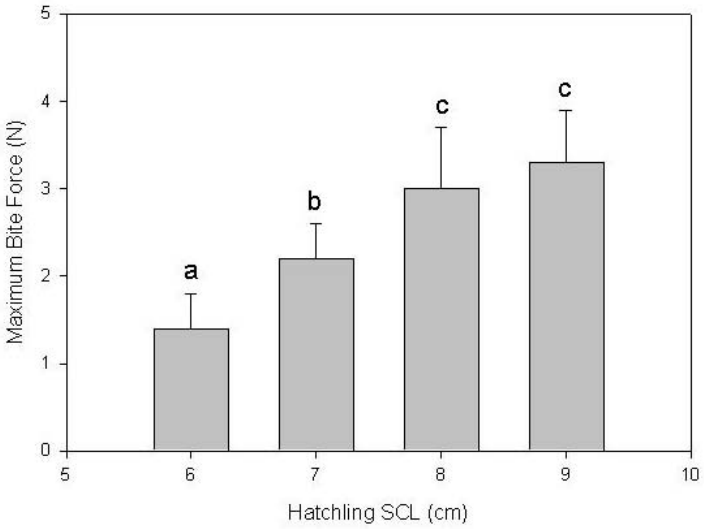

Figure 3. Mean Monthly Post-Hatchling Bite Force. Mean maximum bite force (N) for each size class (cm) from the 4-month post-hatchling study (n=28). Different letters indicate significant differences in bite force between sizes at the 0.001 significance level.

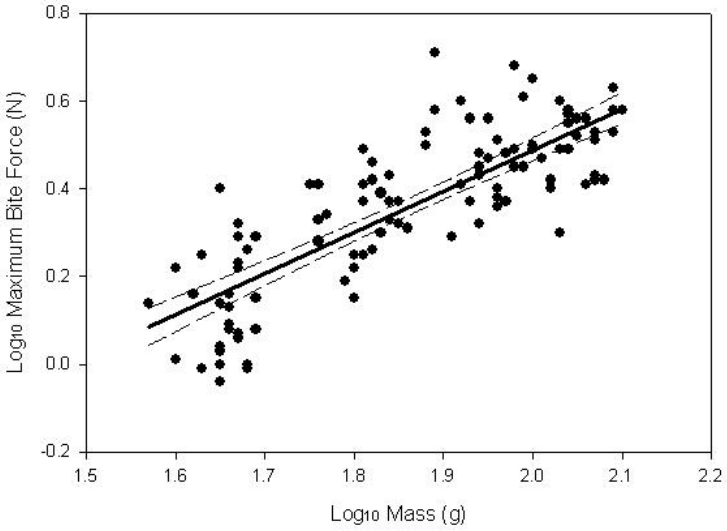

Figure 4. Post-Hatchling Bite Force Regressed Against Mass. Log maximum bite force (N) regressed against log mass (g) for the 4-month study (months three to six) on post-hatchlings (n=28). Regression line and 95% confidence intervals are shown.

Table 1. Post-Hatchling Mean Morphometrics and Maximum Bite Force Values. Values Shown as Means ± Standard Deviation (n=28).

Age	SCL (cm)	CW (cm)	Mass (g)	HW (mm)	HH (mm)	HL (mm)	F_b (N)
3 months	6.4 ± 0.2	5.1 ± 0.2	45 ± 3.0	18 ± 1.0	15 ± 1.0	27 ± 1.0	1.4 ± 0.4
4 months	7.5 ± 0.2	5.9 ± 0.2	65 ± 4.5	20 ± 1.0	17 ± 1.0	30 ± 1.0	2.2 ± 0.4
5 months	8.3 ± 0.3	6.6 ± 0.2	88 ± 6.2	21 ± 1.0	18 ± 1.0	33 ± 1.0	3.0 ± 0.7
6 months	9.2 ± 0.2	7.3 ± 0.3	112 ± 8.1	24 ± 1.0	20 ± 1.0	36 ± 1.0	3.3 ± 0.6

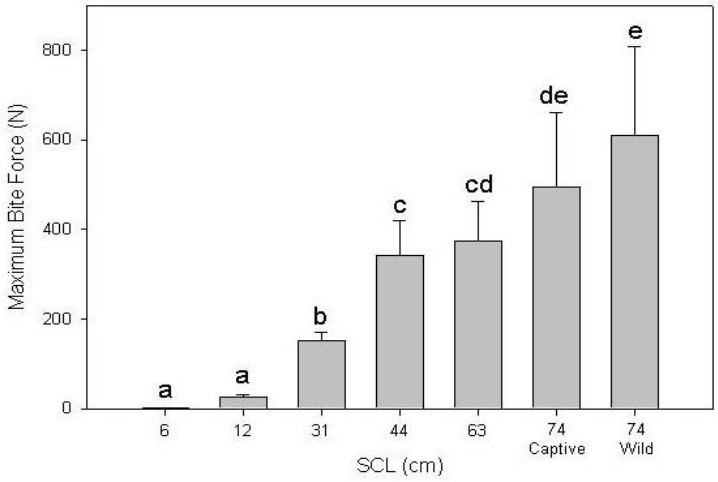

Figure 5. Mean Loggerhead Bite Force by Size Class. Mean maximum bite force (N) for each loggerhead size class measured: post-hatchlings 6 cm mean SCL (n=28), juveniles at 12 cm (n=29), 31 cm (n=30), 44 cm (n=30), and 63 cm (n=24) mean SCL, and captive (N=4) and wild (N=9) sub-adult and adult turtles. Different letters indicate a $P<0.05$ significance level or lower.

classes. Post-hatchling bite force was less than 1% of that measured in the largest juvenile size class (63 cm mean SCL). Bite force was also positively linearly correlated with all body and head morphometrics ($P<0.001$).

In general, body and head morphometrics of juveniles also increased with age and size. In the first year, mean monthly growth was: 19 cm in SCL, 16 cm in CW, 34 mm in HW, 29 mm in HH, 49 mm in HL, and 3.8 kg in mass. The second year mean monthly growth rate decreased, when compared to that of the first year, in all morphometrics except mass: SCL increased 13 cm, CW 10 cm, HW 22 mm, HH 21 mm, HL 34 mm, and mass 6.7 kg. Overall, captive-reared juveniles more than doubled their SCL, CW, HH, HW, and HL within 1 year, and mass increased 15 fold. The 63 cm size class of juveniles nearly doubled in all body and head morphometrics and had over an 8 fold increase in mass when compared to those for the 31 cm size class counterparts. All juvenile turtle morphometrics and bite force data are summarized in Table 2.

Sub-Adults and Adults

Bite force of sub-adult and adult turtles was variable, ranging from 291 to 946 N. Mean maximum bite force of all sub-adult and adult individuals (74 ± 11 cm mean SCL) was 575 N. The largest observed bite force was 946 N from a wild loggerhead (72 cm SCL) caught on a hook and line off a Galveston pier. Maximum bite force of the wild and captive sub-adult and adult turtles was significantly greater than that of all smaller size classes ($P<0.02$), except with the 63 cm SCL size class (Figure 5). An increase of 201 N in bite performance was observed between the largest juvenile size class and the

sub-adult and adult turtles, but this difference was not statistically significant. No difference was detected between the mean maximum bite force among wild (610±200N) and captive (495±165N) sub-adult and adult loggerheads (Figure 5). All morphometrics and bite force values for wild and captive sub-adult and adult turtles are summarized in Table 3.

Morphometric Predictors of Bite Force Throughout Ontogeny

Mean maximum bite force from 6 cm SCL post-hatchlings, 12, 31, 44, and 63 cm mean SCL juveniles, and sub-adult and adult individuals (74 cm mean SCL) was analyzed to investigate further bite force relationships throughout ontogeny.
Bite force increased from 1.4 to 575 N throughout the observed ontogeny, resulting in a 410 fold increase in bite performance. Multiple linear regression analysis demonstrated that carapace width was the best predictor of bite force throughout the observed loggerhead ontogeny ($(LogF_b) = -1.208 + 2.337$ (LogCW); Adj. $R^2 = 0.928$; Figure 6). Maximum bite force values from all loggerhead size classes were regressed against SCL (Figure 7). Power curve estimations best fit the maximum bite force data throughout ontogeny (Adj. $R^2 = 0.922$) suggesting that bite performance is still increasing in the sub-adult and adult turtles measured (Figure 7).

Bite Force Residuals: A Comparison with Other Vertebrates

Bite force residuals were calculated for 132 species of mammals, fish, reptiles, and birds (see Appendix A). Regression analysis resulted in a positively linear trend

Table 2. Juvenile Mean Morphometrics and Maximum Bite Force Values. n= 29 for 9 Month Turtles, n=30 for 20 and 34 Month Turtles, and n=24 for 36 Month Turtles. Values Shown as Means ± Standard Deviation.

Age	SCL (cm)	CW (cm)	Mass (kg)	HW (mm)	HH (mm)	HL (mm)	F_b (N)
9 months	12 ± 0.6	9.7 ± 0.5	0.3 ± 0.0	28 ± 1.0	25 ± 1.0	45 ± 2.0	27 ± 3.4
20 months	31 ± 1.6	26 ± 1.3	4.1 ± 0.6	62 ± 2.0	54 ± 2.0	93 ± 4.2	152 ± 20
34 months	44 ± 3.5	36 ± 2.8	11 ± 2.6	84 ± 5.3	75 ± 5.5	127 ± 8.9	343 ± 78
36 months	63 ± 2.0	50 ± 1.8	33 ± 2.5	109 ± 5.8	93 ± 4.2	166 ± 5.8	374 ± 88

Table 3. Sub-Adult and Adult Morphometrics and Maximum Bite Force Values. Summary of Morphometrics and Observed Bite Force Values for Sub-adult and Adult Wild and Captive Loggerheads of Unknown Ages (n=13).

Turtle ID	Location	Wild (W) or Captive (C)	SCL (cm)	CW (cm)	Mass (kg)	HW (mm)	HH (mm)	HL (mm)	F_b (N)
MJ2004	STI	C	59.4	43.9	28.1	116	101	173	291
JOSH 2004	STI	C	65.2	48.8	35.8	134	112	174	465
GRACIE 2007	STI	W	67.5	52.9	45.4	136	121	187	528
SLM 060928-01	GAL	W	68.9	57.9	40.8	138	125	200	676
BMH 060831-01	GAL	W	69.0	57.6	47.0	126	107	201	633
MADDS 2007	STI	W	70.2	56.5	47.6	143	122	206	433
EES 060807-01	GAL	W	71.6	57.6	52.0	140	291	200	946
KR 070612-01	GAL	W	72.2	58.1	51.5	132	268	209	374
782P	BLA	C	73.6	71.9	60.2	162	139	167	688
RRV 289, 220	GAL	W	75.1	61.4	55.6	141	285	203	887
EES 060823-01	GAL	W	78.2	61.2	63.2	148	297	219	435
YYB018	PSL	W	92.4	71.3	116	187	176	205	583
ATLAS 3103	MGA	C	98.6	68.7	169	197	179	276	535

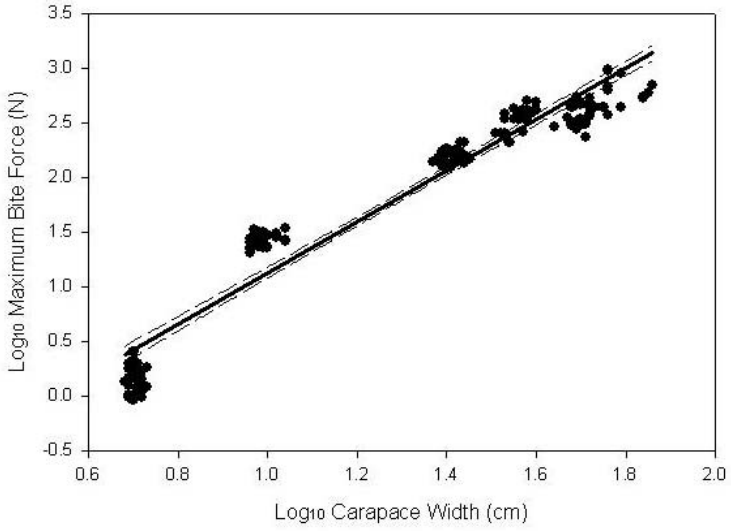

Figure 6. Loggerhead Bite Force Regressed Against Carapace Width. Log maximum bite force for post-hatchlings at 6 cm (n=28) mean SCL, juveniles at 12 cm (n=29), 31 cm (n=30), 44 cm (n=30), 63 cm (n=24) mean SCL, and sub-adult and adult individuals (n=13) regressed against log carapace width (cm). Regression line and 95% confidence intervals are shown.

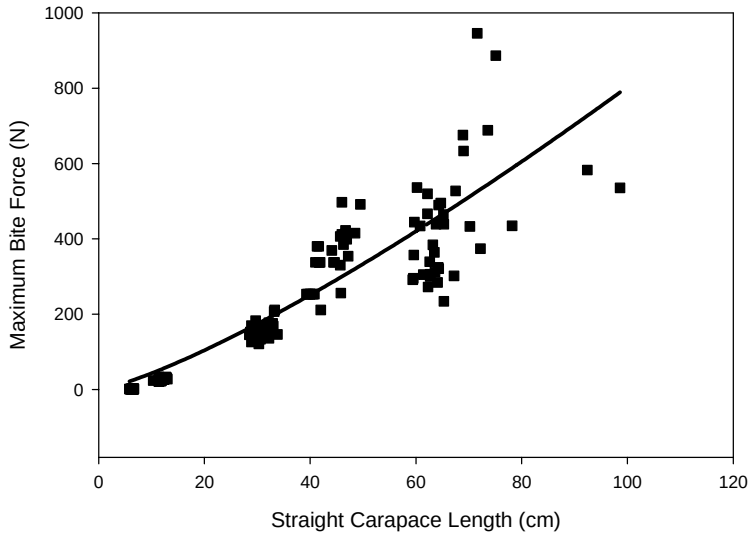

Figure 7. Ontogenetic Bite Force Regressed Against Carapace Length. Bite force values (N) regressed against SCL (cm) for all turtles including post-hatchlings at 6 cm (n=28) mean SCL, juveniles at 12 cm (n=29), 31 cm (n=30), 44 cm (n=30), 63 cm (n=24) mean SCL, and sub-adult and adult individuals (n=13) with the power curve estimation fitted to the data.

between log transformed bite force and mass in all vertebrate species including data from this study and the current literature (Adj. $R^2 = 0.824$; Figure 8A). Residual bite force in the loggerhead size classes examined in this study (6, 12, 31, 44, 63, and 74 cm mean SCL) were -0.84, 0.05, 0.01, 0.1., -0.15, and -0.13, respectively. Therefore, bite force residuals increased from post-hatchling individuals up to the 44 cm SCL juvenile size class where the highest bite force residual was observed. Residual bite force then decreased in the largest two size classes.

Mean residual bite force (available from the literature) of fish, reptiles, birds, mammals, and loggerheads were 0.28, 0.10, -0.07, -0.07, -0.17, respectively. In general, fish had the highest mean bite force residual and loggerheads had the lowest. Although ANOVA resulted in significant differences between bite force residual means among vertebrate groups (P=0.008), Scheffé's *post-hoc* pair-wise comparisons did not show any significant paired differences. However, when loggerheads were included in the reptile group, differences in mean residual bite force were observed between vertebrate groups (P=0.011). Fish had significantly higher bite force residuals when compared to birds (P=0.045) and mammals (P=0.031). When loggerhead bite force residuals were included in the reptile group, the mean bite force residual decreased to 0.06 for reptiles.

Discussion

As expected, loggerhead bite force increased with carapace and head size and mass. Post-hatchling bite force steadily increased within the first few months after birth but was relatively low relative to bite force residual comparisons with other vertebrates.

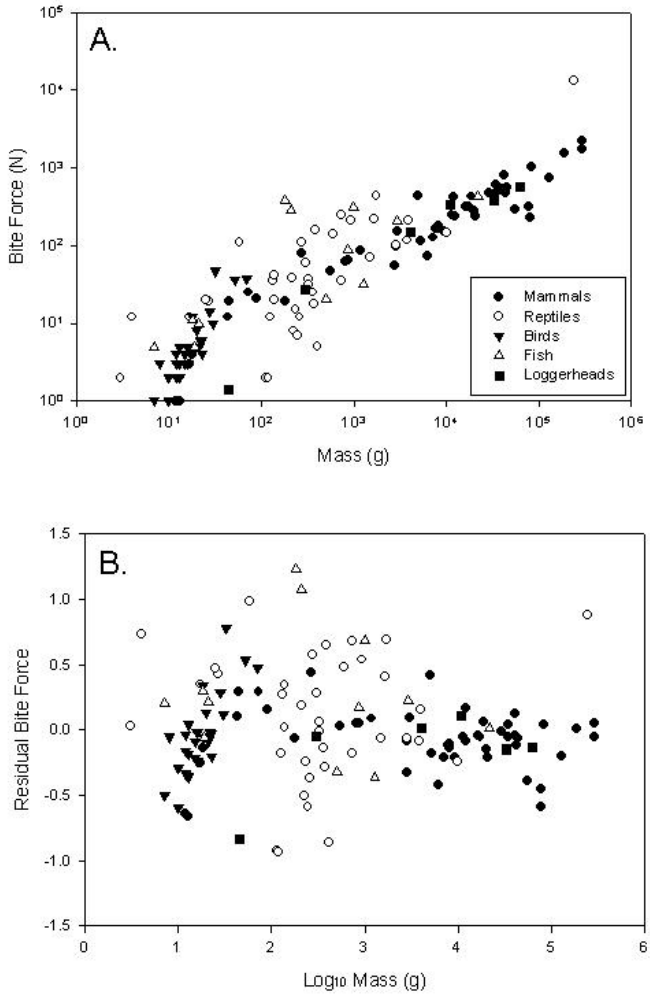

Figure 8. Vertebrate Bite Performance Trends. A. Bite forces (N) of vertebrate groups (for which data were available from the literature) plotted against mass (g). B. Bite force residuals from regression analysis of log transformed bite force versus log transformed mass plotted against log transformed mass (following Huber et al., 2005). Loggerhead data are represented as solid squares.

Early development of lizards and turtles may constrain the head and jaw system and, in turn, bite performance by utilizing all available energy reserves toward differentiation and growth (Herrel and O'Reilly, 2006); therefore selection for higher bite performance may be greater in adults than in juveniles (Herrel and O'Reilly, 2006).

Mean maximum bite force differed significantly in all size classes studied ($P<0.001$) except between the 6 and 12 cm and the 44 and 63 cm mean SCL groups. As previously mentioned, growth was accelerated in the 63 cm SCL size class of captive-reared juveniles. This accelerated growth may explain the lack of differences in bite performance between the 44 and 63 cm SCL size classes. The largest bite force increase was observed between the 31 and 44 cm mean SCL sizes classes. The largest loggerhead bite force measured was 946 N in a wild turtle encountered off the Texas coast. Sub-adult and adult bite force differed when compared to that of all juvenile size classes ($P<0.001$), except between the 63 cm and captive sub-adult and adults.

No difference in bite performance was detected among captive and wild sub-adult and adult turtles. It was predicted that differences in diet (i.e. soft bodied prey versus hard-shelled prey) would result in different bite performance between similar sized sub-adult and adult captive and wild loggerheads; however, these data suggest the use of soft bodied prey and a pellet diet used in captive-rearing programs and rehabilitating centers did not negatively affect loggerhead bite performance in this study.

Bite Performance and Ontogenetic Shifts in Diet

Although these data demonstrated that oceanic sized loggerheads (<60 cm SCL) have lower bite performance than do neritic individuals (> 60 cm SCL), the data do not give sufficient information to determine if this increase in bite force is due to increase in body size or to ontogenetic changes in skull and jaw morphology as a result of diet differences. Residual bite force, accounting for mass, was highest in the 44 cm mean SCL size class. This size group, along with the 63 cm SCL size class, would presumably be on the verge of the ontogenetic shift in the wild. The bite performance data suggest that bite force has not yet reached a plateau and is still increasing in the largest sub-adults and adults measured.

Increased bite performance may provide ecological advantages such as an increase in the prey spectrum toward more energy rich items (Herrel et al., 1999a, 2001b, 2002). The observed bite force measurements for sub-adult and adult loggerheads suggest individuals presumably feeding on benthic hard-shelled prey are capable of biting harder than juvenile loggerheads. However, this study lacks the bite performance data from loggerhead size classes (>60 cm) on the edge of the presumable shift from oceanic to neritic environments to clearly show a biomechanical ontogenetic shift that is coupled with a habitat shift to coastal environments. Additional bite performance data are needed from larger sub-adult and adult individuals before making any conclusions regarding the relationship between bite performance and ontogenetic shifts in habitat and diet.

Although alligators (*Alligator mississippiensis*) typically exhibit ontogenetic shifts in diet (Dodson, 1975) similar to those in loggerheads, an investigation of their bite force throughout ontogeny demonstrated that their pattern of bite force increases are not associated with trophic shifts (Erickson et al., 2003), as one would expect. Adult loggerheads (30-50 cm SCL) presumably living on the continental shelf in Japanese and Mediterranean waters, inhabit both neritic and oceanic habitats (Hatase et al., 2002; Cardona et al., 2005) and seldom exploit benthic prey (Revelles et al., 2007). Therefore, this typical ontogenetic shift in habitat and diet in loggerheads may not be as dramatic as originally thought, which may explain some of the variability of bite force patterns observed in this study. Habitat shifts may allow loggerheads to exploit different prey types, which ordinarily would not be available, and increased bite performance would be an advantage for efficient feeding particularly on hard-shelled benthic prey.

Bite Force Predictors

The morphometric variables that best predict bite performance vary among vertebrates. In this study, mass was the best predictor of bite force in post-hatchling loggerheads, whereas carapace width was the best bite force predictor throughout subsequent loggerhead ontogeny. As a result, body morphometrics, instead of head morphometrics, are most closely correlated with loggerhead bite performance. Another study examining bite force throughout alligator ontogeny had similar results. In alligators, total body length had the strongest relationship with bite force (Erickson et al., 2003). These, along with findings from this study, suggest that bite force is most closely

associated with body dimensions, as opposed to head dimensions as reported in other reptilian species, particularly throughout ontogeny (Herrel et al., 2001a, 2001b, 2002; Verwaijen et al., 2002; Herrel and O'Reilley, 2006).

Head dimensions are strongly correlated with bite force in several freshwater turtle species (Herrel and O'Reilly, 2006), such as *Chelydra serpentina,* omnivorous snapping turtles (Ernst et al., 1994), and *Staurotypus triporcatus* and *S. salvini*, carnivorous musk turtles (Pritchard, 1979). These findings are surprising since the size of freshwater turtle heads are constrained due to the need to fit their head back in their shell (Herrel et al., 2002). However, carapace length was most closely correlated to bite force throughout ontogeny in *Trachemys scripta*, the red-eared slider that is carnivorous as a juvenile and omnivorous as an adult (Clark and Gibbons, 1969); however, once body dimensions were excluded from the regression analysis, head width was the best bite force predictor (Herrel and O'Reilly, 2006). In lizards, head morphometrics, specifically head width and head height, are also most closely related to bite performance possibly due to the location of the jaw musculature (Herrel et al., 2001a, 2001b; Verwaijen et al., 2002; Herrel and O'Reilly, 2006). Loggerhead head width was also a reasonable predictor of bite force after carapace width and mass.

Comparisons to Other Vertebrates

Bite force residuals based on maximum bite force and body mass were calculated for 132 species from different vertebrate groups (following Huber et al., 2005; See Appendix A) in order to examine how loggerhead bite performance compares to that

observed in other vertebrates,. The residuals accounting for body mass could then be compared between species and vertebrate groups. Some of the largest calculated vertebrate bite force residuals resulted from Canary Island lizards (*Gallotia galloti*), American alligators, hogfish, (*Lachnolaimus maximus*), and striped burrfish (*Chilomycterus schoepfi*) (Herrel et al., 1999a; Erickson et al., 2005; Clifton and Motta, 1998; Korff and Wainwright, 2004). The mata mata (*Chelus fimbriatus*), red-bellied short neck turtle (*Emydura subglobosa*), and post-hatchling loggerheads exhibited the lowest residual bite force (Herrel et al., 2002). Loggerhead residual bite force is largest in the 44 cm SCL compared to that for the other loggerhead size classes; however, the bite force residuals for all size classes, excluding the low residual calculated in post-hatchlings (6 cm SCL), are average with respect to all bite force residuals from other vertebrate species.

In a comparison with bite force measured from several freshwater turtle species (Herrel et al., 2002), post-hatchling and small juvenile ($\leq$ 31 cm SCL; approximately the same size as the adult freshwater species) loggerhead bite performance was greater than that for all herbivorous and omnivorous turtles except *Chinemys reevesii*, Reeve's turtle, an omnivore. Observed bite force from post-hatchling and small juvenile loggerheads is much lower that most similar sized durophagous or carnivorous freshwater turtles, with the exception of the common musk turtle, *Sternotherus odoratus*. Juvenile loggerheads ($\leq$ 40-60 cm SCL) in the wild are omnivorous which would explain the low bite performance compared to durophagous or carnivorous turtles, and the higher bite performance compared to herbivorous freshwater turtles. These data suggest there may

be an increasing bite force trend with respect to diet. Therefore, it is predicted that bite performance may be lowest in herbivorous species and highest in carnivorous or durophagous species, as suggested by the comparisons between freshwater turtles and loggerheads.

The ontogeny of alligator bite force allows for a comparable assessment with that for loggerheads (Erickson et al., 2003). Alligators, which attain sizes much larger than the loggerheads studied, have higher residual bite force in small and large individuals when compared to loggerheads. Alligator and loggerhead ontogenetic bite force trends, related to body size, appear to both exhibit exponential increases in bite performance.

Concluding Remarks

This study is the first to measure bite performance in any marine turtle species. In summary, loggerhead bite force increased throughout ontogeny. The largest increase was observed between the 31 and 44 cm SCL size classes and the highest bite force residual occurred in the 44 cm SCL. Although it is predicted that loggerheads are powerful biters due to their durophagous feeding ecology during their coastal life stage, bite force was lower than expected when compared to that of other vertebrates, after size has been taken into account. Bite force residuals suggested that loggerhead bite force throughout the observed ontogeny falls within the range of other vertebrates, and is not exceptionally high. However, hatchings have one of the lowest calculated residuals. This may be a result of post-hatchlings focusing their energy reserves toward differentiation and growth. Whereas head morphometrics best predict bite force in

smaller reptilian species, body morphometrics best predict loggerhead bite force which may be true in large reptilian species.

Loggerhead bite force increased throughout the entire observed ontogeny and dramatic increases in bite force were observed in increasing size classes; however bite performance never reached a plateau throughout the observed ontogeny. More bite performance data are needed to make more concrete statements about the link between bite performance and ontogenetic shifts in habitat and diet, typical of loggerheads. Increased loggerhead bite performance will only render this species vulnerable to the longline fishery if higher bite performance increases the likelihood of becoming hooked on longline gear which may causes a higher probability of these turtles drowning.

CHAPTER III

LOGGERHEAD INTERACTIONS WITH BAITED LONGLINE HOOKS: A KINEMATIC AND BEHAVIORAL ANALYSIS

Introduction

Although aquatic feeding appears stereotypical both within and between species (Lauder and Shaffer, 1985; Shaffer and Lauder, 1985; Reilly, 1995), it has been suggested that feeding kinematics may be modulated based on prey type (Lauder and Prendergast, 1992; Lemell and Weisgram, 1997; Bels et al., 1998; Deban and Wake, 2000) and environment (Summers et al., 1998). Various studies have examined the kinematics of aquatic feeding vertebrates such as hagfish (Clark and Summers, 2007), ray-finned fish (eg., Liem, 1990; Gibb, 1995, 1996, 1997; Wainwright, 1996; Wintzer and Motta, 2005; Higham et al., 2006; Beck and Turingan, 2007), sharks (Wilga et al., 2007), salamanders (Shaffer and Lauder, 1985; Findeis and Bemis, 1990; Reilly and Lauder, 1989, 1998; Gillis and Lauder 1994; Reilly, 1995), frogs (Dean, 2003), and marine mammals (Werth, 2000a, 2000b; Bloodworth and Marshall, 2005; Marshall et al., 1998, 2000, 2003) with an emphasis on suction feeding capabilities and evolutionary patterns in vertebrate feeding kinematics. The kinematic profile, with respect to timing and head movement variables (jaw opening, hyoid depression, mouth closing) of suction feeding vertebrates is conserved, particularly in relation to the hyoid apparatus. This may be a result of hydrodynamic properties and constraints (Bramble, 1973; Lauder, 1985; Van Damme and Aerts, 1997).

Feeding kinematics have been studied in several aquatic and marine turtle species (Bramble, 1973, 1978; Lauder and Prendergast, 1992; Bels and Renous, 1992; Van Damme and Aerts, 1997; Lemell et al., 1997, 2002; Bels et al., 1997, 1998; Summers et al., 1998; Lemell and Weisgram, 2000); however, no studies have investigated aquatic feeding kinematics and behavioral variables with explicit conservation implications.

The fate of sea turtles that interact with longline gear is poorly understood (Bjorndal et al., 1999a; Chaloupka et al., 2004; Sasso and Epperly, 2007); as a result, more studies must focus on understanding the complex interactions between sea turtles and the longline fisheries. Feeding behavior that leads to turtle hooking may be dependent upon hook type, hook size, hook offset, bait, and bait presentation. Some studies have demonstrated that changing longline fishing gear can significantly decrease harmful turtle interactions without significantly affecting targeted fish catch (Bolten et al., 2002; Garrison, 2003; Watson et al., 2003, 2004a, 2004b, 2005; Bolten and Bjorndal, 2005). Based on these studies, it is predicted that larger circle hooks (18 gage) with the largest offset (10˚) baited with fish species should be most effective in decreasing harmful turtle-longline interactions.

Increased concern for the survival of sea turtle populations and the conflicting findings from past longline studies mandate that more information regarding how loggerheads interact with the longline fishery be gathered before implementing effective longline management strategies or longline gear modifications. Therefore, the objectives of this study are to: 1) characterize loggerhead feeding kinematics; and 2) compare kinematic and behavioral data between circle and J hooks of various sizes and offset

angles. Kinematic and behavioral differences in feeding relative to hook treatment were measured to test the hypotheses that: 1) loggerhead feeding behavior is modulated relative to hook treatment; 2) circle hooks resulted in fewer harmful turtle interactions; and 3) hook offset reduces the incidence of throat hooking.

Materials and Methods

Subjects

Video trials were conducted from December 2006 to April 2007 on seven captive-reared loggerheads (SCL= 40-55 cm) housed at the NOAA Fisheries Service Galveston sea turtle facility (Galveston, Texas, USA). Individuals were moved to a 2,000 L fiber glass tank (Red Ewald Inc., Karnes City, TX, USA) with glass windows installed on two sides to record underwater feeding from lateral and frontal perspectives. Air temperature was approximately 21-24˚C and water temperature was approximately 24-27˚C during filming. Turtles were allowed 15 minutes to acclimate to the holding tank before feeding trials and filming began.

High speed video recordings of loggerheads feeding from baited longline hooks were obtained using a Redlake PCI Motion Scope camera at 250 frames s^{-1}. Each subject was recorded interacting with five barb-less hook treatments: J hook (9 gage) with 25˚offset (J-25), 16 gage circle hook with no offset (16-0), 16 gage circle hook with 10˚ offset (16-10), 18 gage circle hook with no offset (18-0), and 18 gage circle hook with 10˚ offset (18-10) (Lindren-Pitman Inc., Pompano Beach, FL, USA). All turtle-safe hooks were modified to ensure no turtle would swallow the hook or

otherwise be harmed. Hook barbs were ground down and the remaining hook was covered with plastic shrink tubing and secured with plastic ties (Figure 9). Hook leaders were made with 68 kg (150 lb) clear monofilament line and crimped sleeves commonly used in longline fisheries. Hooks were attached to a wooden platform, and the platform was clamped onto the tank edges to ensure consistent and stationary hook location. Squid were double threaded onto each hook prior to securing the plastic shrink tubing with plastic ties. All efforts were made to mimic actual longline fisheries gear.
Five lateral and five frontal views (10 feeding events) were recorded separately for each of the five hook treatments (10 feeding events x 5 hook treatments = 50 events per individual). Seven turtles were filmed feeding from each of the hook treatments for a total of 350 total recorded feeding events (7 turtles x 50 events/turtle). Lateral events were analyzed only if the turtle's head was parallel or nearly parallel to the filming window during feeding. During recording, 1,000-1,500 watts of lighting were used for illumination.

Kinematic and Behavioral Variables

Lateral and frontal feeding events were digitized using Motus 8.2 (Vicon Motion Systems, Denver, CO, USA). The following ten kinematic variables were analyzed from each feeding event, with the frame immediately before mouth opening defined as time zero: 1) maximum gape (cm), the greatest distance between tips of the upper and lower jaw; 2) duration of gape opening (ms), the duration between time zero and maximum gape; 3) duration of gape closing (ms), the duration between maximum gape to the time

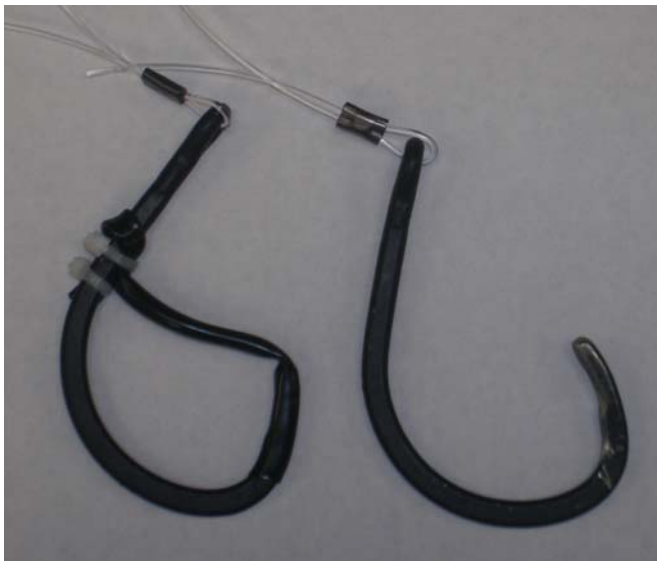

Figure 9. Turtle Safe Longline Hooks**.** Size 18 barb-less circle hooks without offset were used in this study. The hook on the left shows the use of plastic shrink tubing and plastic ties used to ensure no turtle would be able to swallow the hook or otherwise be harmed.

the rhamphotheca closed onto the baited hook; 4) maximum gape angle (degrees), the maximum angle determined from the maxillary tip of the upper jaw, to the mouth commissure point (vertex), to the tip of the dentary; 5) maximum hyoid depression (cm), the greatest vertical displacement of the hyoid determined as the difference between the maximum and minimum distance relative to the lateral commissure of the eye; 6) time to maximum hyoid depression (ms), the duration between time zero and maximum hyoid depression; 7) duration of gape cycle (ms), duration between time zero and the time the rhamphotheca closed onto the baited hook; 8) maximum velocity of gape angle opening (degrees/second), the greatest angular rate of jaw opening; 9) maximum velocity of gape angle closing (degrees/second), the greatest angular rate of jaw closing; and 10) angular orientation of head relative to hook (degrees), determined by the angle from the top of the hook, to the hook bottom (vertex), to the maxillary tip of the upper jaw (roll). All kinematic variables were analyzed from lateral views of feeding (Figures 10A and 10B) except for the angular orientation of the head relative to the hook (roll), in which case frontal views of feeding events were used (Figure 10C). Digitizing schematics are illustrated in Figure 10.

In addition, the following five behavioral variables were analyzed: 1) proportion of hooked events, determined by the number of hooked events in relation to total number of feeding events; 2) hooking location frequency; determined by the number of events from each hook location category (mouth or throat) relative to the total number of hooked events; and 3) proportion of turtles that orient the dorsal portion of their head and tip of their maxillary straight ahead, left, or to the right direction of the hook, and

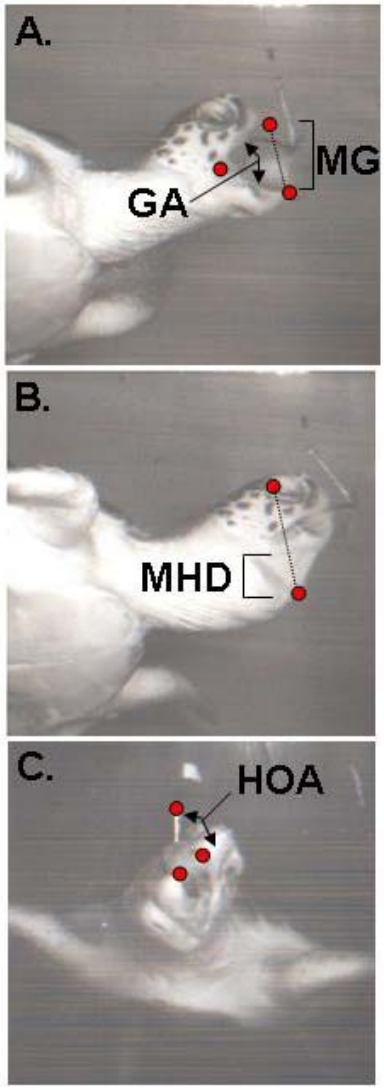

Figure 10. Digitized Points and Spatial Models**.** Digitized points and spatial models overlaid on lateral and frontal video frames. Kinematic variables collected from the lateral views were A. maximum gape angle (GA), the angle formed from the tip of the maxillary on the upper jaw, to the mouth commissure (vertex), to the tip of the dentary; maximum gape, the maximum distance from the tip of the maxillary to the tip of the dentary; and B. maximum hyoid depression (MHD), determined as the difference between the maximum and minimum distance from the lateral commissure of the eye to the hyoid point. C. Angular head orientation to the hook (HOA) was collected from the frontal view of the feeding event and was determined as the angle from the top of the hook, to the bottom of the hook (vertex), to the tip of the maxillary.

toward, straight, or away from the hooks with an offset (J-25, 16-10, and 18-10; Figure 10), determined by the number of events for each head orientation category (left, straight, right or toward, straight, away) in relation to total number of feeding events. Turtles were considered hooked if the barb-less part of the hook entered the turtle's oral cavity when a turtle closed its jaw over the hook. This would presumably result in the hook barb piercing through the turtle's rhamphotheca or skin within the buccal cavity, if a real hook barb was used. All feeding events, even those not recorded with the high speed camera (n=2,541), were used to determine hooking frequency; therefore not all feeding events resulted in hooked events. Only hooked events were recorded for kinematic analysis.

Hooking location was defined as the location of the barb-less hook in the oral cavity that would likely be penetrated if a real hook barb was used. Instances where the entire hook was positioned within the turtle's mouth (i.e. little or no shrink wrap observed) was considered to be a throat hooking while those events where only the hook tip is positioned within the turtle's oral cavity was considered to be a mouth hooking. Hook orientation was controlled in all feeding trials. Hooking location was evaluated from the lateral perspective. The tip of the hook barb was facing the turtle during all feeding and filmed events. From the frontal perspective, the hook barb could not be seen from hooks without offset (16-0 and 18-0); however the hook offset from the J-25 hook was always oriented 25˚ to the left of the hook and the 16-10 and 18-10 hooks were always oriented 10˚ to the right of the hook when analyzed in video recordings (see Figure 11 for clarification). When feeding from the J-25 hook, if turtles oriented their

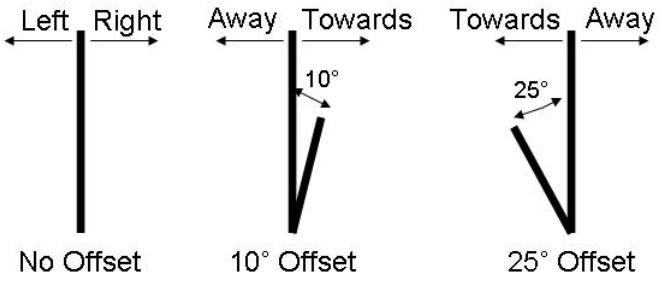

Figure 11. Hook Offset from the Frontal Perspective. A schematic figure of the hooks with and without offset from the frontal perspectives of the video recordings. Hook barbs from hooks without offset (16-0 and 18-0) were not noticeable in the frontal perspective. Hook barbs from the J-25 hook were always oriented 25˚ to the left while hook barbs from both the 16-10 and 18-10 hooks were always oriented 10˚ to the right. This schematic also illustrates how the head orientation categories were determined (i.e., left or right when feeding from hooks without offset and toward or away from the hook offset). These behaviors were analyzed to determine head orientation frequencies to the hook and the hook offset.

head and upper jaw tip to the left of the hook, this resulted in a head orientation toward the offset; however, when feeding from the 16-10 and 18-10 hooks, if turtles oriented their head and upper jaw tip to the left of the hook, this resulted in head orientation away from the hook offset. Head orientation was considered straight in all hook treatments when the turtles head was nearly parallel with the top of the hook. The frequencies of head orientation toward the hook (with 0˚ offset) and hook offset (10˚ and 25˚) were analyzed.

Statistical Analyses

Normality and variance homogeneity were tested for all kinematic variables using the Kolmogorov-Smirnov and Levene tests, respectively. Kinematic variables that did not meet normality or variable homogeneity were $\log_{10}$ transformed. Size effects were removed by regressing all kinematic variables against SCL. These residuals were then used in statistical tests for all kinematic variables (Zar, 1999). Since each turtle was recorded interacting with each hook five times, a repeated measures one factor analysis of variance (ANOVA) was utilized to examine individual variability. An ANOVA, using kinematic means per turtle, was performed on all kinematic variables to detect differences between the five hook treatments, followed by Scheffé's *post-hoc* analyses to determine which pair wise or multiple comparisons were significantly different (Zar,1999). Although ANOVA tests are robust against departures of both normality and heterogeneity of variances (Zar, 1999), kinematic variables that did not meet these assumptions (duration of gape opening, duration of gape closing, duration of gape cycle,

and head orientation angle), even after transformations, were analyzed using a Kruskal-Wallis non-parametric test. Paired t-tests were used to compare kinematic variables associated with opening and closing of the mouth (time and velocity). All behavioral variables were analyzed using a chi-squared goodness of fit test to determine if observed frequencies differed significantly from expected or theoretical frequencies between categories (Zar, 1999), and *post-hoc* chi-squared pair-wise comparisons were examined within categories as described in Cox and Key, (1993). SPSS (version 14.0) was used for all statistical analyses. Significance for all statistical procedures was accepted at the $P<0.05$ level.

Results

Kinematic Profile

A typical feeding event consisted of the turtle moving forward toward the baited hook with a closed mouth. The feeding event began as the turtle opened its mouth. Hyoid depression began at the end of mouth opening and maximum depression was attained after maximum gape. During the onset of mouth closing, most turtles closed their eyes. The end of the feeding event was characterized by the turtle closing its mouth over the hook. Mean total gape cycle duration was 856 ± 326 ms. Mean duration of gape opening (696 ± 314 ms) differed significantly from mean duration of gape closing (160 ± 55 ms) and was approximately four times longer in duration ($P<0.001$). Mean maximum gape was 6.5 ± 0.9 cm and mean maximum gape angle was $48 \pm 7.9^{\circ}$. Mean opening and closing gape angle velocities were $611 \pm 182^{\circ}\ s^{-1}$ and $854 \pm 239^{\circ}\ s^{-1}$,

respectively, with these differing significantly ($P<0.001$); closing gape angle velocity was approximately 40% faster. Hyoid depression began during mouth closing and attained maximum depression toward the end of the feeding event. Mean maximum hyoid depression was 4.3 ± 0.9 cm. Time to maximum hyoid depression (803 ± 334 s) significantly differed from total gape cycle duration ($P<0.001$). Mean angular head orientation to the hook was $34^{\circ} \pm 18^{\circ}$, although values varied (1-84˚). A typical lateral and frontal feeding sequence are illustrated in Figures 12 and 13. No differences were detected within or between subjects in any of the kinematic variables analyzed in relation to the five hook treatments.

Behavioral Variables

Only 34% of all feeding events resulted in hooked interactions (Table 4). Chi-squared results indicated there was a significant difference in the proportion of hooked and not hooked interactions between hook treatments ($P<0.001$; Figure 14A). The lowest proportion of hooked events occurred when turtles interacted with 16-0 hooks (30%) and 18-10 hooks (30%); conversely, the highest proportion of hooking occurred when interacting with 16-10 hooks (45%; Table 4). Chi-squared pair-wise comparisons demonstrated that 16-10 hooks differed significantly from all other hook treatments with respect to hooked and not hooked proportions ($P<0.025$).

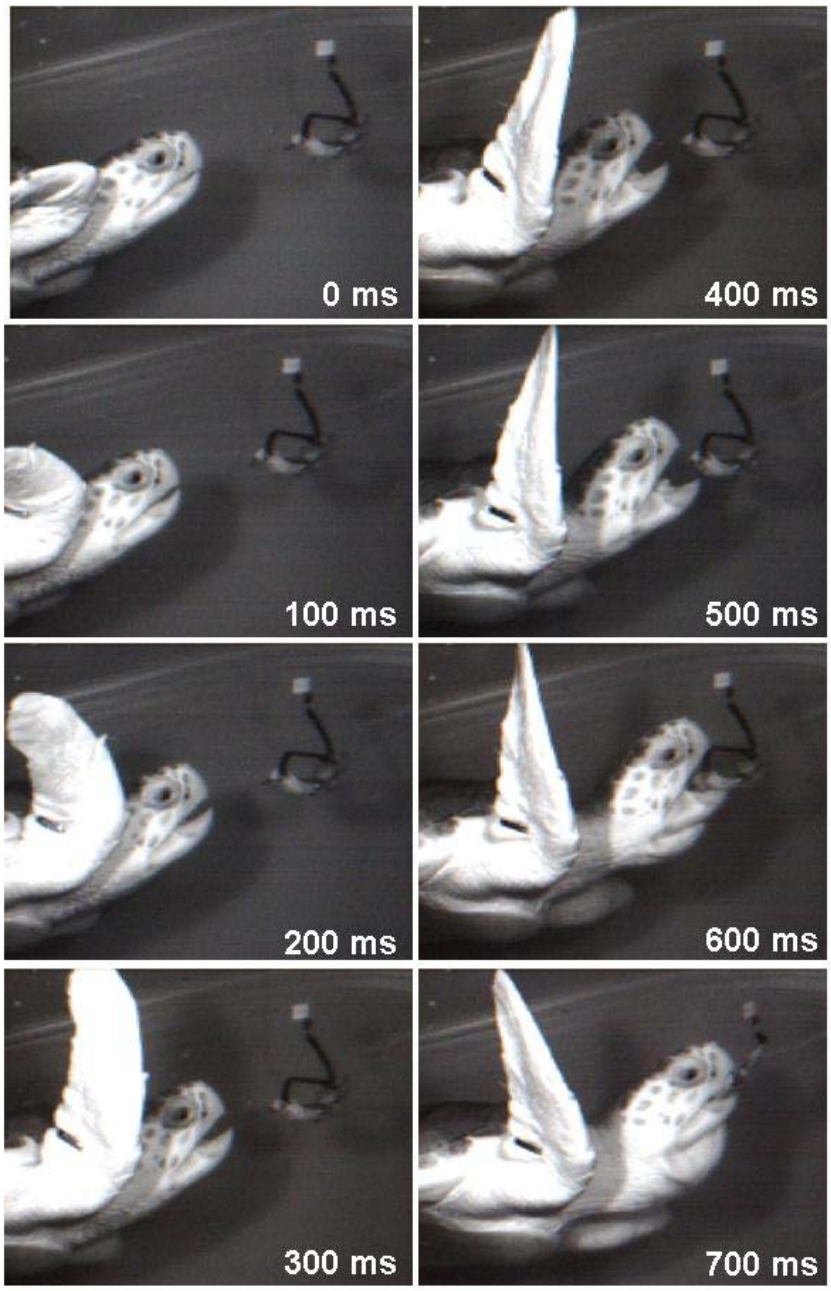

Figure 12. Lateral Feeding Sequence. Representative video frames from the lateral perspective starting at time zero to the end of the gape cycle when the turtle closed its mouth over the hook. Time is shown every 100 ms. Interaction with the 18-10 circle hook is shown.

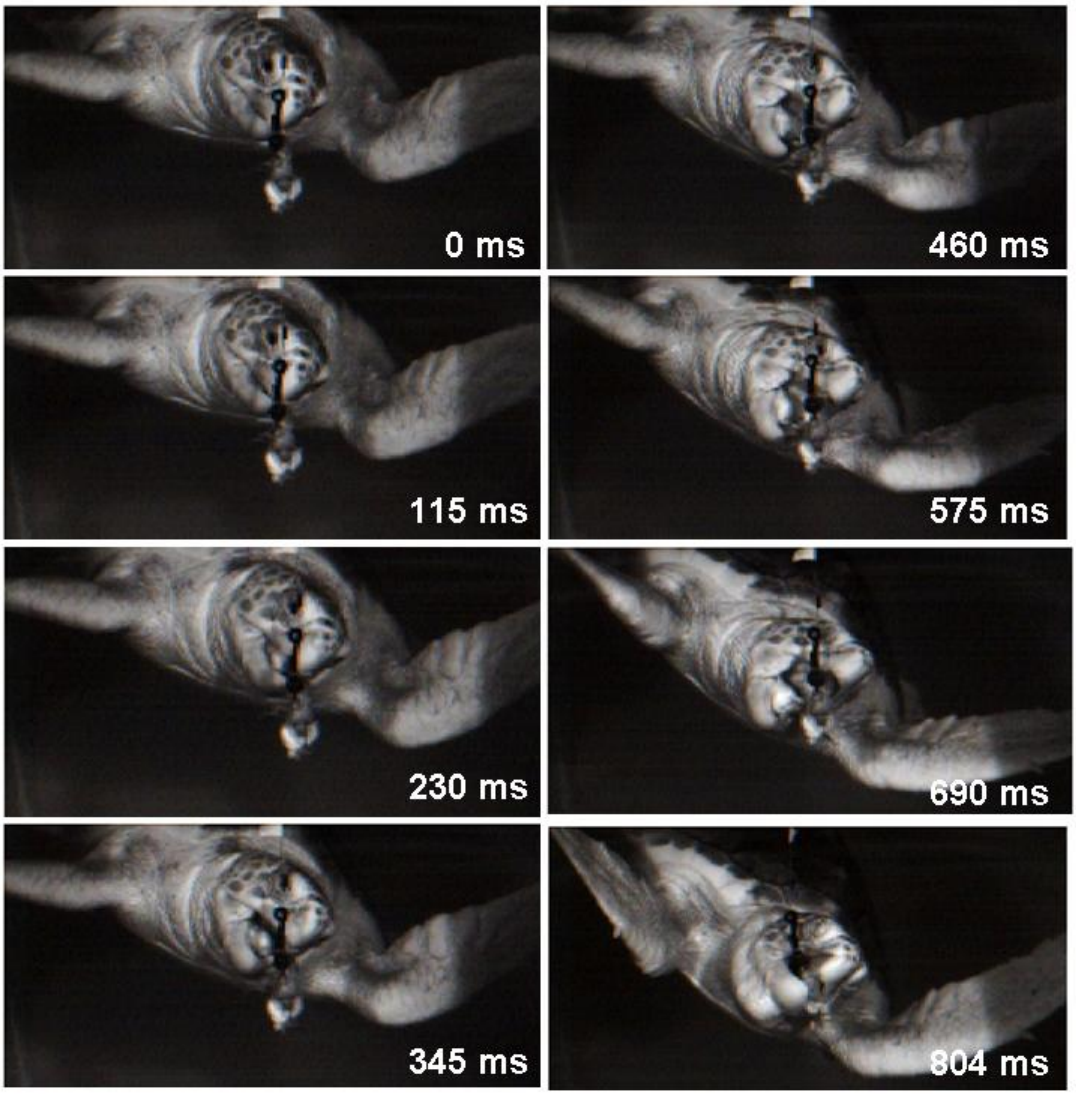

Figure 13. Frontal Feeding Sequence. Representative video frames from the frontal perspective starting at time zero to the end of the gape cycle when the turtle closed its mouth over the hook. Time is shown every 115 ms. Interaction with the 18-0 circle hook is shown.

Proportions of hooking location, either mouth or throat, differed between hook treatments (P=0.001; Figure 14B). Most interactions with the baited longline hooks resulted in mouth hooking (67%; Table 4). In all hook treatments, frequency of throat hooking was lower than frequency of mouth hooking. The proportion of throat hooking was lowest in the 18-0 hook interactions (21%) and highest in 16-10 hook interactions (48%; Table 4). Pair-wise comparisons resulted in significant differences in proportions of throat hooking between the 16-10 hook and all other hook treatments ($P<0.025$) and between the J-25 and 18-0 hooks ($P<0.05$).

The proportion of head orientation toward the hook (i.e. left, right or straight) differed significantly between hook treatments ($P<0.001$). A closer look at all feeding events demonstrated that turtles mainly oriented their heads to the right of the hook (50%) when compared to left (37%) or straight (13%) head orientations (Table 4). Since significant differences were observed in head orientation frequencies, further separate analyses were conducted to investigate head orientation frequencies in hooks without offset (16-0 and 18-0) and hooks with offset (J-25, 16-10, and 18-10). No differences were observed in head orientation (i.e., left, right, or straight) frequencies in hooks without offset, and similar frequency trends were observed in both these hook treatments (Figure 15A); however analyses on head orientation frequency resulted in significant differences in these head orientation proportions when feeding from hooks with offset (P=0.04) suggesting these proportions differ than expected values and are not due to chance. Further investigations examined head orientation to the hook offset rather than

Table 4. Behavioral Variable Frequencies. Behavioral Results Analyzed with Chi-Squared Goodness of Fit Tests for Each Hook Treatment and for the Total Number of Feeding Events. All Values are Expressed as Percentages.

Behavioral Tests	Behavior Categories	J-25	16-0	16-10	18-0	18-10	Total
Hooking	Hooked	36.4	29.7	45.2	31.9	29.9	33.8
	Not Hooked	63.6	70.3	54.8	68.1	70.1	66.2
Hooking Location	Throat	31.7	40.6	48.3	21.3	28.5	32.9
	Mouth	68.3	59.4	51.7	78.7	71.5	67.1
Head Orientation to Hook	Straight	5.3	22.0	10.5	14.5	14.1	13.1
	Left	17.5	48.0	31.6	51.6	35.2	36.7
	Right	77.2	30.0	57.9	33.9	50.7	50.2
Head Orientation to Hook Offset	Straight	5.3	-	12.1	-	14.1	10.8
	Towards	17.5	-	56.9	-	50.7	42.5
	Away	77.2	-	31.0	-	35.2	46.8

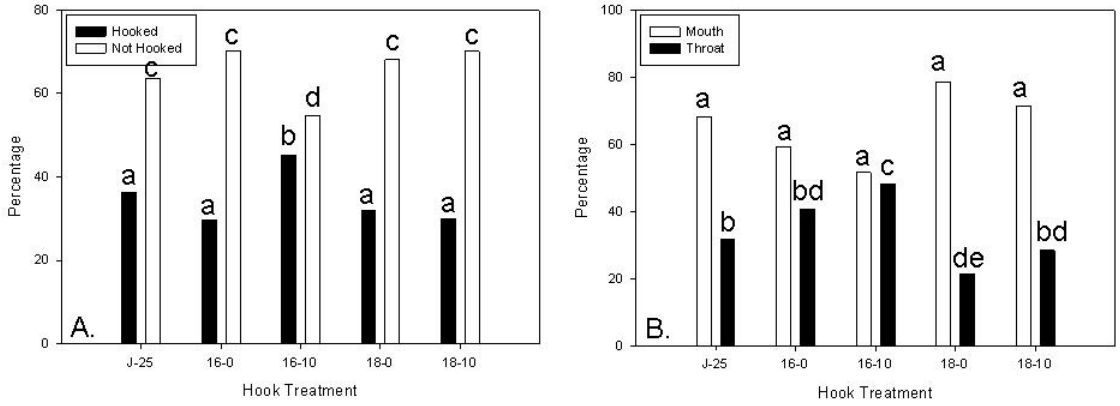

Figure 14. Hooking and Hook Location Proportions. A. The proportion of feeding events resulting in hooked and not hooked interactions for all hook treatments based on total number of feeding events. Different letters indicate significant differences among hooked or not hook proportions at the 0.025 significance level. B. The proportion of feeding events resulting in mouth and throat hooking for all hook treatments based on total number of interactions. Different letters indicate significant differences among mouth and throat proportions at the 0.05 level or below.

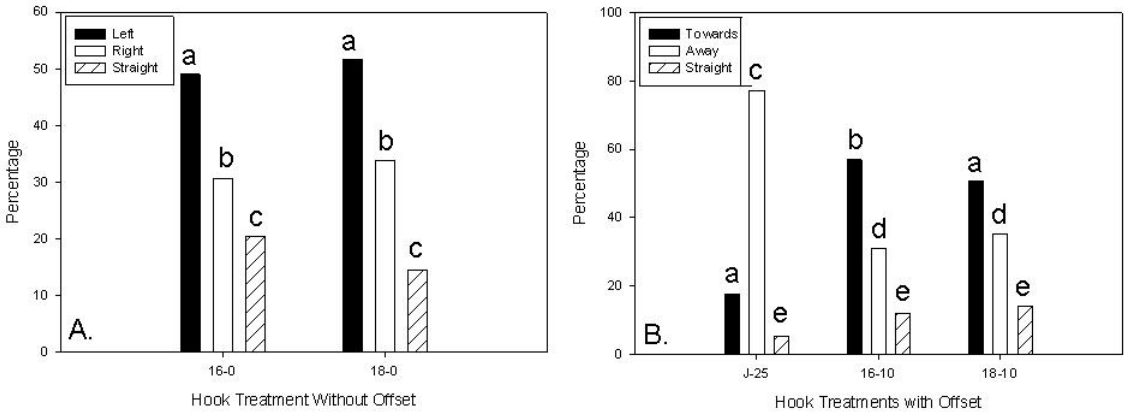

Figure 15. Head Orientation Frequencies Toward Hook and Hook Offset. A. The proportion of feeding events where turtles oriented their heads toward the left, right or straight onto the hooks without offset based on frontal perspectives. B. The proportion of feeding events where turtles oriented their heads toward, away from or straight onto the hook offset based on frontal views. Different letters indicate significant differences among head orientation toward the hook offset at the 0.025 significance level or lower.

the hook itself since the J and circle hooks had offsets pointing in different directions (J-25 to the left and 16-10 and 18-10 to the right; Figure 11).

When examining feeding events from hooks with offsets, 47% of turtles oriented themselves away from the hook offset, 43% oriented themselves toward the hook offset, and 11% oriented themselves straight onto the hook, with these percentages differing significantly between hook treatments ($P<0.001$; Figure 15B). When turtles interacted with the J-25 hook, a larger proportion of turtles oriented themselves away from the hook offset (77%) compared to head orientations straight on (5.3%) or toward the hook offset (18%). However, when interacting with 16-10 and 18-10 hooks, turtles oriented their heads toward the hook offset 57 and 51%, respectively. Pair-wise *post hoc* comparisons found significant differences in the proportion of turtles that oriented themselves away from the hook between the J-25 and both the 16-10 and 18-10 hooks ($P<0.005$). Significant pair-wise differences were detected between the 16-10 and both the J-25 ($P<0.025$) and 18-10 hooks ($P<0.01$) with respect to head orientation to the hook offset. All behavioral results are summarized in Table 4.

Discussion

Feeding Kinematics

Aquatic feeding is the ancestral condition in all vertebrates, but terrestrial feeding is ancestral in all amniotes (Lauder, 1985; Bramble and Wake, 1985). Therefore, all turtles, like marine mammals, are tetrapods that have secondarily returned to the aquatic environment (Bramble and Wake, 1985). Aquatic feeding in turtles evolved from a

feeding apparatus adapted for a terrestrial environment (Lauder and Prendergast, 1992). Basic morphological design of the terrestrial feeding apparatus in vertebrates appears to differ dramatically from aquatic feeding models (Liem, 1990). More studies should investigate feeding in both the terrestrial and aquatic surroundings since some kinematic studies in freshwater turtles suggest otherwise. One study suggests that feeding behavior is conserved between species in both environments (Bels et al., 1998) while another study suggested that feeding within the same species differs between both environments with respect to maximum gape and hyoid depression (Summers et al., 1997). Since sea turtles have secondarily returned to the marine environment, investigations provide insights regarding the evolution of amniote feeding and of the feeding apparatus with respect to terrestrial versus aquatic environments.

No differences were detected in loggerhead feeding kinematics with respect to the different hook treatments. These data suggest that loggerhead feeding is stereotypical when interacting with stationary or slow moving prey. Sterotypical feeding kinematics has been observed in aquatic feeding freshwater turtles (Bramble, 1978; Lauder and Prendergast, 1992), marine turtles (Bels et al., 1998), salamanders (Reilly and Lauder, 1989; Findeis and Bemis, 1990; Reilly, 1995), and frogs (Dean, 2003). However, some studies suggest that feeding behavior can be highly variable (Van Damme and Aerts, 1997) and modulated based on prey type (Lauder and Prendergast, 1992; Bels et al., 1998; Deban and Wake, 2000) or environment (Summers et al., 1998).

Suction feeding behavior is heavily dependant on the morphology of the skull, jaws, hyobranchial apparatus, gill slits, and tongue (Deban and Wake, 2000). Typical

suction feeding involves rapid mouth opening, attainment of peak gape, and peak hyoid depression occurs after the mouth has been closed (Lauder, 1985; Deban and Wake, 2000; Lemell et al., 2002). This sequence of feeding events, where mouth opening peaks before maximum hyoid depression, and the associated bell shaped gape profile, observed in loggerhead feeding kinematics, is also observed in many aquatic feeding vertebrates (Lauder, 1985; Shaffer and Lauder, 1985; Lauder and Prendergast, 1992; Bels and Renous, 1992; Reilly, 1995; Bels et al., 1997; Deban and Wake, 2000; Werth, 2000a; Lemell et al., 2002). Aquatic feeding freshwater turtles appear to have similar feeding kinematics as primary aquatic feeding vertebrates (Van Damme and Aerts, 1997).

The duration of loggerhead feeding cycles in this study was longer than reported for most fish, salamanders, and freshwater turtles (Shaffer and Lauder, 1985; Lauder and Shaffer, 1985; Lauder and Prendergast, 1992; Gillis and Lauder, 1994; Reilly, 1994; Gibb, 1995, 1996, 1997; Van Damme and Aerts, 1997; Bels et al., 1997, 1998; Summers et al., 1998; Lemmel et al., 2002; Winzter and Motta, 2005; Beck and Turningan, 2007). However, size or differences in water temperature across studies (19-28˚C) may account for this variability. Comparisons of kinematic data from two marine mammal species, demonstrate that loggerhead feeding cycle duration is similar to that of *Tursiops* (a ram feeder) but longer than that of *Kogia* (a suction feeder; Bloodworth and Marshall, 2005). In most fish and aquatic salamanders, jaw opening is shorter in duration than jaw closing (Lauder, 1983, 1985). Duration of jaw opening is approximately twice as that of jaw closing (Lauder, 1985). These timing patterns are also observed in most freshwater

turtle species (Lauder and Prendergast, 1992) where the duration of gape closing can last approximately 2-4 longer than that of the gape opening (Lemell et al., 2002). However, this timing pattern was not observed in loggerhead sea turtles.

The duration of gape opening in the loggerhead kinematic profile was approximately four times longer than that of the gape closing. Not surprisingly, closing gape angle velocity was also significantly faster than the opening gape angle velocity ($P<0.001$). These data suggest that loggerheads, unlike most aquatic feeding vertebrates, have a rapid jaw closing phase and gape angle closing velocity relative to jaw opening. Similar closing durations have been observed in one species of marine turtle (Bels et al., 1998), freshwater turtle (Bels et al., 1997), and aquatic frog (Dean, 2003). Dean (2003) suggested a faster gape closing phase may be beneficial to avoid prey loss during water flow reversal in bidirectional feeding systems exhibited by turtles and frogs. Similar to that in loggerheads, the opening gape angle velocity in bottlenose dolphins was also faster than closing gape angle velocity (Bloodworth and Marshall, 2005). Bloodworth and Marshall (2005) suggested that faster gape angle closing velocities are characteristic of ram feeding aquatic vertebrates, due to the need of effectively capturing elusive prey.

Ram feeding is the most common form of prey capture in aquatic feeding turtles (Bramble, 1978; Lauder and Prendergast, 1992; Summers et al., 1998); although the freshwater turtle species, *Chelodina* and *Pelusios,* and the leatherback sea turtle exhibit inertial suction capabilities during prey capture or prey manipulation (Lemell and Weisgram, 1997; Van Damme and Aerts, 1997; Bels et al., 1998). Suction feeding in turtles is similar to suction feeding observed in aquatic premetamorphic salamanders and

fish (Lauder, 1985). Although this study did not measure pressure directly, loggerheads exhibited ram feeding behavior and compensatory suction that prevents the forward motion of the predator from pushing the prey away. Since aquatic feeding in turtles is bidirectional, their movements toward prey must be accompanied by compensatory suction in order to successfully overcome the prey (Van Damme and Aerts, 1997).

Aquatic feeding turtles are capable of storing water in their esophagus to compensate for a bidirectional system (Lauder, 1985). Lauder (1985) termed this adaptation, esophageal expansion. The increased volume of water entering the mouth is thought to aid in compensatory and inertial suction feeding (Van Damme and Aerts, 1997). In one species of aquatic frog, maximum hyoid depression followed mouth closure, which may be an adaptation to effectively overcome bidirectional feeding constraints (Dean, 2003).

Profiles of hyoid depression are similar among aquatic vertebrates (Lauder and Prendergast, 1992). The hyoid apparatus is the most conserved part of the aquatic feeding system possibly due to the hydrodynamic constraints of aquatic feeding (Lauder and Shaffer, 1985; Shaffer and Lauder, 1985). Hyoid depression produces a rapid increase in buccal cavity volume during jaw opening that is used by compensatory and inertial suction feeders. Although no pressure data were collected in this study, the large hyoid depression suggests that loggerheads are capable of using compensatory suction when interacting with the stationary baited hooks. However, inertial suction was observed during preliminary feeding trials with dead shrimp and squid; electrophysiological experiments that measure pressure profiles of feeding loggerhead

turtles should be collected to confirm the suction capabilities of loggerheads. Such capabilities will have important implications regarding hook ingestion.

Behavioral Variables

Although the kinematic profile of loggerhead feeding appears stereotypical, behavioral variables resulted in distinct differences between hook treatments. The 16-0 and 18-10 hooks resulted in the lowest percentage of "hooking." These results may suggest that the probability of a turtle drowning, due to hooking, would be lowest when feeding from these two types of baited hooks in the longline fishing industry. Hook offset did not appear to have a main affect on hooking frequency. Throat hooking was lowest in the 18-0 hook and highest in the 16-10 hook. Behavioral responses to circle hooks suggest that hook offsets increase the proportion of throat hooking. The 16-10 hooks resulted in the most harmful turtle interactions with respect to both hooked and hooking location while 18-0 and 18-10 hooks yielded the fewest harmful turtle interactions. Alternatively, these results could be an artifact of the smaller size of the 16 gage circle hooks compared to that of the 18 gage circle hooks. However, 16-0 hooks did not result in increased hooking events. As a result, there appears to be an interaction between size and hook offset that influences frequency of hooking. Although the results support clear differences between the five hook treatments, it is unclear whether these findings are a result of loggerheads modulating their feeding behavior based on hook type or simply differences in hook design.

Previous studies have demonstrated that J hooks result in high sea turtle swallowing rate (i.e., throat hooking) when compared to that from circle hooks (Bolten and Bjorndal, 2005; Watson et al., 2005). Circle hooks appear to decrease sea turtle-longline fishery interactions, the frequency of hook swallowing, and presumably, post-hook mortality (Watson et al., 2003, 2005; Bolten and Bjorndal, 2005; Gilman, 2006); however, use of circle hooks is not always the most effective measure in decreasing the number of harmful turtle-longline interactions (Bolten et al., 2002; Bolten and Bjorndal, 2005). The J hook (9 gage) treatment in this captive study did not result in the largest proportion of hooked or throat interactions, as reported in field tests (Watson et al., 2003, 2004b, 2005; Bolten and Bjorndal, 2005). Since loggerheads oriented their heads away from the hook offset when interacting with hooks with a large offset (25°) and toward the hook offset when interacting with a hook with a small offset (10°), these data suggest they may be able to distinguish between large and small offsets and adjust their behavior accordingly. Alternatively, loggerheads may not be able to distinguish between hooks with no offsets or those with relatively minimal offsets.

Concluding Remarks

In summary, loggerheads exhibit a similar kinematic profile when compared to that of other aquatic feeding vertebrates. However, loggerheads had longer gape cycle durations and a faster jaw closing duration and jaw closing velocity. These feeding characteristics may be typical of ram feeding aquatic vertebrates to avoid prey loss. Although pressure data were not collected in this study, it appears that loggerheads are

capable of both compensatory and inertial suction feeding. Loggerhead feeding appears stereotypical when feeding from different baited longline hooks. The 16-10 circle hook resulted in the most harmful interactions while 18-0 and 18-10 circle hooks yielded the lowest frequency of hooked events and throat interactions, which presumably would lead to less turtle drownings. Loggerheads do appear to distinguish between small (10˚) and large (25˚) offsets and modulate their feeding behavior accordingly. Further investigations of loggerhead feeding biomechanics, such as suction performance studies, as well as longline fishery gear interactions with fish bait and other bait threading methods, should be conducted to fully understand the complex interactions between loggerhead feeding behavior, hook type, and bait.

CHAPTER IV

CONCLUSION

Feeding ecology and behavior likely contribute to loggerheads' vulnerability to capture in the longline fishery. This study is the first to characterize loggerhead bite performance throughout ontogeny. Mean maximum bite force of post-hatchlings (6-10 cm SCL) was 2.5 N with mean monthly increases of 0.8 N except between 5 and 6 months of age when an increase of 0.3 N was observed. Mass was the best predictor of post-hatchling bite force. Mean maximum bite force of juvenile loggerheads with mean SCL of 12, 31, 44, and 63 cm was 27, 152, 343, and 374 N, respectively. Mean maximum bite force of sub-adult and adult turtles (74 cm mean SCL) was 575 N, and the largest recorded bite force value was 946 N from a wild Texas gulf coast turtle (72 cm SCL). Maximum bite force significantly differed in all loggerhead size classes ($P<0.001$) except between the 44 and 63 cm SCL juveniles. No difference in bite force was observed in similar sized wild and captive sub-adult and adult individuals. Bite force had a positive linear correlation with all body and head morphometrics, and carapace width was the best predictor of bite force throughout observed ontogeny. The power curve estimation best fit the ontogenetic bite performance data suggesting bite force is still increasing in the observed ontogeny measured in this study.

Loggerhead feeding kinematics and behavior were analyzed from recorded interactions of loggerheads feeding on different squid baited longline hooks. For all kinematic variables analyzed, no difference was detected between hook treatments indicating loggerhead feeding kinematics may be stereotypical. Only 34% of all

interactions resulted in hooked events and of these hooked events, 33% resulted in throat hookings. Hooking percentage was lowest in the 16-0 and 18-10 hooks. Throat hooking frequency was lowest when turtles interacted with the 18-0 hook. The 16-10 hook resulted in the highest proportion of hooked events and throat hookings. When interacting with hooks with larger offsets (J-25) turtles oriented their heads away from the hook barb more often; however, when interacting with hooks with small offsets (16-10 and 18-10) turtles oriented their heads toward the hook barb most often. These data suggest that turtles can distinguish between large and small offsets and modulate their feeding behavior accordingly.

Interactions between sea turtles and the longline fishery have become a growing concern (Ross, 1995; Hillestad et al., 1995; Lewison et al., 2004). Juvenile loggerheads that interact with the longline fishery are presumably the size classes that are beginning to recruit to neritic foraging grounds (Kotas et al., 2004; Bolten and Bjorndal, 2005). As a result, interactions with the longline fishery may be decreasing the recruitment of sea turtles particularly in the western Atlantic (Bolten and Bjorndal, 2005). Therefore, new and effective longline management strategies must be implemented soon before sea turtle populations are threatened any further.

Longline management strategies must not only be effective, but also commercially viable (Gilman, 2006). Many studies have examined ways to decrease sea turtle bycatch associated with the longline fisheries. Some suggestions to decrease the number of hooked interactions and the proportion of swallowed hooks (i.e. throat hooking) include the implementation of large circle hooks (Watson et al., 2003, 2004a,

2004, 2005; Bolten and Bjorndal, 2005; Gilman et al., 2006), decreasing hook offset (Watson et al., 2004b), the use of fish bait (Watson et al., 2003, 2004b, 2005; Gilman, 2006), dying bait (Swimmer et al., 2007), avoidance of turtle hotspots (Marvovaldi et al., 2006), fishing further away from the coast (Báez et al., 2007), retrieving sets earlier in the day (Bolten and Bjorndal, 2005), eliminating shallow longline sets (Polovina et al., 2003; Báez et al., 2007), and banning the use of light sticks (Witzell, 1999; Wang et al., 2007); however, not all recommendations have been effective or successfully implemented. With respect to gear and bait modifications, some suggestions have resulted in maintained or higher catch per unit effort (CPUE) for targeted swordfish and tuna catch (Watson, 2003, 2004a, 2004b, 2005; Gilman, 2006) while other recommendations have resulted in lower targeted CPUE for some tuna species (Watson, 2004a; 2004b). Gilman et al. (2006) believe fishery specific changes dependant on turtle size, bycatch species, and the type of fishery will be most successful, although this may entail further research efforts.

This work on loggerhead bite performance and feeding kinematics was an attempt to directly link performance, ecology, and morphology in loggerheads to better understand the complex interaction between loggerheads and longline fishery gear as a means to decrease future sea turtle bycatch. Increased bite performance changes associated with the ontogenetic shift in diet and habitat typical of loggerheads would only render this species vulnerable to the longline fishery if it occurred in pelagic juveniles (< 60 cm SCL). Bite force increased with each size class studied, although loggerhead bite performance residuals are comparable to those of other vertebrates. As a

result of this bite force trend in comparison to other vertebrates, loggerhead bite performance may not be a characteristic of their natural history that renders this species vulnerable to the longline fishery.

I expected the rate of bite force development to increase exponentially within the 40-60 cm SCL sized turtles and reach a plateau in the sub-adult and adult individuals. However, the bite performance data were measured from turtle size classes that are on the verge of this transition from pelagic to neritic habitats. Due to the increasing bite force trend throughout observed ontogeny and the variability in bite performance in sub-adult and adult turtles, more bite force data are needed from larger turtles to make any concrete statements about the relationship between bite performance and ontogenetic diet changes. The data from this study will enable future work to target the specific size classes necessary to characterize the biomechanical and habitat ontogenetic shift, if it does occur.

This study on loggerhead feeding kinematics suggests that loggerhead feeding is stereotypical and similar to that of other aquatic feeding vertebrates. Based on feeding observations, loggerheads appear to use a combination of ram feeding methods, associated compensatory suction, and biting for feeding. These conclusions are supported by fast gape closing durations and gape closing angle velocities that would presumably aid in efficient prey capture. However, anecdotal evidence from this study suggests that loggerheads may possess inertial suction capabilities which may play a role in hook ingestion (i.e. throat hooking) within the longline fishery.

Our investigation of loggerheads feeding from baited longline hooks suggests that size, as opposed to hook offset, may be most effective at decreasing harmful turtle interactions. The behavioral data suggest that larger circle hooks would be the most effective at decreasing negative sea turtle interactions. This may be a result of the larger size of the hook where a larger turtle gape would be necessary to become hooked or specifically hooked in the throat. There was not enough evidence to determine the role of hook offset in this complex loggerhead-longline interaction. Loggerheads do appear to modulate their feeding behavior toward or away from the hook offset depending on the angle of the offset. Loggerheads only appear to distinguish between large offsets (25˚), as noted by their head orientation. However, it is not clear if these behavioral differences are a result of loggerheads modulating their feeding behavior toward the different hooks, or simply due to the differences in hook design (i.e. hook type, size, offset). In conclusion, there seems to be a complex interaction between hook size and hook offset that should be further investigated. The experimental setup used in this study to film loggerheads feeding from baited longline hooks can be used in the future to examine feeding behavior, from loggerheads or targeted fish species, with respect to new hook designs or gear modifications.

Future Work

This study is the first to characterize loggerhead feeding behavior in detail by investigating bite performance and the kinematic feeding profile. Due to the accessibility of juvenile loggerheads at the NOAA Fisheries Galveston facility, future

longitudinal bite force studies could measure a subset of individuals throughout their entire stay at the facility (i.e. 3 years). If bite force was measured from the same turtle every month for three years, the exact rate and development of juvenile bite force could be determined accounting for individual variation. The relationship between bite force, gape angle, and biting point (anterior versus posterior biting) could also be further investigated. Maximum theoretical bite performance values could be obtained through stimulation studies of the jaw musculature, and these data could be combined with information regarding the relationships between bite force, gape angle, and biting point to develop a biomechanical model of loggerhead biting; however, these maximum theoretical values may be difficult to investigate due to the threatened status of loggerhead sea turtles.

Since bite force data were mostly measured from juvenile loggerheads ($\leq$ 60 cm SCL), which presumably would be oceanic, opportunistic omnivores, bite force data from larger sub-adult and adult turtles (> 60 cm SCL) are needed. These measurements would allow greater insight on how bite performance is related to ontogenetic shifts in loggerhead diet and habitat and to determine if clear shifts in observed bite performance are associated with these ontogenetic shifts. This data will add to current information on loggerhead natural history. Future ecomorphological studies could investigate the relationship between ecology and performance by determining the force required to crush some of the hard shelled, benthic prey species which loggerheads typically consume during their neritic life stage, and examine how these values are related to observed loggerhead bite performance. Although this study is the first to measure bite

force in any marine turtle species, in the future, observed bite performance values can be compared between sea turtles to examine how similarities or differences in diet and feeding ecology between sea turtle species may affect bite performance.

Loggerhead feeding kinematics and interactions between loggerheads and longline fishing gear were investigated in a controlled setting. Although this study did not examine suction in detail, compensatory and inertial suction was observed in this study, therefore future work may examine loggerhead suction capabilities. Future studies might investigate how different bait and bait threading methods affect sea turtle feeding from baited longline hooks. The laboratory setting used in this study is ideal to evaluate how loggerheads respond to and interact with new longline hook designs; therefore this method could be used to test future hook designs or modifications in order to obtain preliminary information and results on sea turtle feeding kinematics and behavior before implementing any gear modifications within the longline fishery. This study is the first attempt to fully understand the complex interactions between sea turtles and longline fishing gear in a controlled setting. More data are severely needed to better understand these relationships before an effective and efficient longline management strategy can be implemented which could diminish sea turtle bycatch.

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APPENDIX A

VERTEBRATE BITE FORCE RESIDUALS

Vertebrate Group	Scientific Name	Common Name	Bite Force (N)	Mass (g)	Residual Bite Force	Source
Mammals	*Homo sapiens*	Human	294	55,000	-0.39	(Ringqvist, 1972)
	Rattus norvegicus	Norway rat	47	555	0.03	(Robins, 1977)
	Didelphis virginiana	North American opossum	442	5,000	0.42	(Thomason et al., 1990)
	Crocuta crocuta	Spotted hyena	242	20,700	-0.21	(Binder and Van Valkenburgh, 2000)*
			2195	292,000	0.05	
	Monodelphis domestica	Short-tailed opossum	21	90	0.16	(Thompson et al., 2003)
	Acinonyx jubatus	Cheetah	475	29,500	-0.01	(Wroe et al., 2005)
	Alopex lagopus	Artic fox	178	8,200	-0.10	
	Canis alpinus	Dhole	314	16,500	-0.04	
	Canis aureus	Golden jackal	165	7,700	-0.12	
	Canis latrans	Coyote	275	19,800	-0.15	
	Canis lupus dingo	Dingo	313	17,500	-0.06	
	Canis lupus hallstromi	Singing dog	235	12,300	-0.09	
	Canis lupus lupus	Grey wolf	593	34,700	0.04	
	Dasyurus maculates	Spotted-tailed quoll	153	3,00	0.10	
	Dasyurus viverrinus	Eastern quoll	65	870	0.05	
	Felis concolor	Cougar	472	34,500	-0.06	
	Felis sylvestris	Wild cat	56	2,800	-0.32	
	Felis yagouaroundi	Jaguarundi	127	7,100	-0.21	
	Gennetta tigrinum	Striped genet	73	6,200	-0.42	
	Hyaena hyaena	Brown hyena	545	40,800	-0.04	
	Lycaon pictus	African hunting dog	428	18,900	0.06	

	Lynx rufus	Bobcat	98	2,900	-0.09	
	Meles meles	European badger	244	11,400	-0.05	
	Neofelis nebulos	Clouded leopard	595	34,400	0.04	
	Panthera leo	Lion	1768	294,600	-0.05	
	Panthera onca	Jaguar	1014	83,200	0.04	
	Panthera pardus	Leopard	467	43,100	-0.12	
	Panthera tigris	Tiger	1525	186,900	0.01	
	Proteles cristatus	Aardwolf	151	9,300	-0.21	
	Sarcophilus harrisii	Tasmanian devil	418	12,000	0.17	
	Thylacinus cynocephalus	Tasmanian wolf	808	41,700	0.13	
	Urocyon cineroargentus	American grey fox	114	5,300	-0.18	
	Ursus americanus	Black bear	751	128,800	-0.20	
	Ursus arctos	Brown bear	312	77,200	-0.45	
	Ursos thibetanus	Asiatic bear	244	11,400	-0.05	
	Vulpes vulpes	Red fox	164	8,100	-0.14	
	Sus domestica	Domestic Pig	230	80,000	-0.59	(Ström and Holm, 1992)
	Canis familiaris	Labrador Dog	550	45,000	-0.06	
	Pteropus vampyrus	Large flying fox	85	1,167	0.09	(Dumont and Herrel, 2003)
	Pteropus poliocephalus	Grey-headed flying fox	63	820	0.05	
	Eidolon helvum	African straw-colored fruit bat	78	272	0.43	
	Rousettus aegyptiacus	Egyptian rousette	19	179	-0.07	
	Phyllostomus hastatus	Spear nosed bat	25	72	0.29	
	Cynopterus brachyotis	Lesser short-nosed fruit bat	12	44	0.10	
	Artibeus jamaicensis	Jamaican fruit eating bat	19	45	0.29	
	Erophylla sezekorni	Buffy flower bat	3	17	-0.25	
	Monophyllus	Greater	1	13	-0.66	

	redmani	Antillean long-tongued bat				
	Carollia perspicillata	Short-tailed fruit bat	4	18	-0.14	
	Glossophaga soricina	Common long-tongued bat	1	12	-0.64	
Reptiles	*Caiman crocodilus*	Spectacled caiman	70	1,500	-0.06	(Cleuren et al., 1995)
	Gallotia galloti	Canary Island lizard	109	58	0.99	(Herrel et al., 1999a)
	Xenosaurus grandis	Knob-scaled lizard	12	17	0.35	(Herrel et al., 2001a)
	Xenosaurus newmanorum	Crevice-dwelling lizard	19	27	0.43	
	Xenosaurus platyceps	Crocodile lizard	20	25	0.47	
	Amyda cartilaginea	Asian softshell turtle	210	937	0.54	(Herrel et al., 2002)
	Apalone ferox	Florida softshell turtle	2	114	-0.93	
	Apalone spinifera	Spiny softshell turtle	12	260	-0.37	
	Callagur borneoensis	Painted terrapin	147	10,065	-0.24	
	Chelus fimbriatus	Mata mata	5	405	-0.86	
	Chelydra serpentine	Snapping turtle	209	3,940	0.16	
	Chinemys reevesii	Reeve's turtle	20	137	0.02	
	Dogania subplana	Malayan softshell turtle	37	328	0.06	
	Elseya novaeguineae	New Guinea snapping turtle	35	743	-0.18	
	Emydura subglobosa	Red-bellied short-necked turtle	2	119	-0.94	
	Geoemyda	Black	12	126	-0.18	

	spengleri	breasted leaf turtle				
	Heosemys grandis	Giant Asian pond turtle	102	2,866	-0.07	
	Kinosternon scorpioides	Scorpion mud turtle	38	214	0.19	
	Kinosternon subrubrum	Mississippi mud turtle	35	133	0.28	
	Macrochelys temminckii	Alligator snapping turtle	158	388	0.65	
	Orlitia borneensis	Malaysian giant turtle	117	3,818	-0.08	
	Pelodiscus sinensis	Chinese softshell turtle	59	305	0.28	
	Pelomedusa subrufa	African helmeted turtle	8	224	-0.50	
	Phyrnops nasutus	Common toad-headed turtle	432	1,752	0.69	
	Platemys platycephala	Twist-necked turtle	7	245	-0.58	
	Platysternon megacephalum	Big-headed turtle	42	137	0.35	
	Staurotypus salvinii	Pacific coast giant musk turtle	252	743	0.68	
	Staurotypus triporcatus	Mexican giant musk turtle	139	600	0.48	
	Sternotherus carinatus	Razorback musk turtle	109	276	0.58	
	Sternotherus odoratus	Common musk turtle	31	321	-0.01	
	Terrapene carolina	Box turtle	25	361	-0.13	
	Testudo horsfieldii	Russian tortoise	18	373	-0.29	
	Trachemys scripta	Common slider turtle	15	235	-0.24	
	Alligator mississippiensis	American alligator	217	1,650	0.40	(Erickson et al., 2004)*
			13,172	242,700	0.88	
	Podarcis muralis	Common wall lizard	12	4	0.73	(Herrel et al., 2001b)

	Lacerta vivipara	Viviparous lizard	2	3	0.03	
	Caretta caretta	Loggerhead sea turtle	1.4	45	-0.84	Present study*
			27	300	-0.05	
			152	4,100	0.01	
			343	11,000	0.10	
			374	33,000	-0.15	
			575	62,477	-0.13	
Birds	*Amadina erythrocephala*	Red-headed finch	4	23	-0.21	(Van der Meijj and Bout, 2004)
	Amadina fasciata	Cut-throat finch	5	19	-0.06	
	Carduelis chloris	European greenfinch	14	28	0.29	
	Cardeulis flammea	Common redpoll	3	13	-0.18	
	Cardeulis sinica	Grey-capped greenfinch	8	20	0.13	
	Cardeulis spinus	Eurasian siskin	3	13	-0.18	
	Carpodacus erythrinus	Common rosefinch	6	22	-0.02	
	Chloebia gouldia	Gouldian finch	4	15	-0.09	
	Eophona migratoria	Yellow-billed grosbeak	36	52	0.53	
	Erythrura trichroa	Blue-faced parrotfinch	5	13	0.04	
	Estrilda troglodytes	Black-rumped waxbill	1	7	-0.49	
	Hypargos niveoguttatus	Peter's twinspot	3	16	-0.23	
	Lagonosticta senegala	Red-billed firefinch	1	7	-0.49	
	Lonchura fringilloides	Magpie munia	5	16	-0.01	
	Lonchura pallida	Pale-headed munia	3	13	-0.18	
	Lonchura punctulata	Scaly-breasted munia	4	12	-0.03	
	Mycerobas affinis	Collared grosbeak	38	70	0.48	
	Neochima	Plum-	2	13	-0.36	

	modesta	headed finch				
	Neochima ruficauda	Star finch	2	12	-0.34	
	Ceochima ruficauda	Java sparrow	10	30	0.12	
	Padda oryzivora	Long-tailed finch	3	8	-0.05	
	Phoephila cincta	Black-throated finch	3	16	-0.23	
	Pyrrhula pyrrhula	Eurasian bullfinch	5	21	-0.08	
	Pytilia hypogrammica	Red-faced pytilia	3	15	-0.22	
	Rhodopechys obsoleta	Desert finch	6	23	-0.03	
	Serinus leucopygius	White-rumped seedeater	2	10	-0.29	
	Serinus mozambicus	Yellow-fronted canary	3	12	-0.16	
	Serinus sulphuratus	Brimstone canary	12	18	0.34	
	Taenopygia bichenovi	Double-barred finch	2	10	-0.29	
	Taenopygia guttata	Zebra finch	4	23	-0.21	
	Uraeginthus bengalus	Red-cheeked cordonblue	1	10	-0.59	
	Geospiza fortis	Medium Ground Finch	47	32	0.78	(Herrel et al., 2005)
Fish	*Archosargus probatocephalus*	Sheepshead	309	998	0.69	(Hernandez and Motta, 1997)
	Halichoeres bivittatus	Slippery dick	5	19	-0.06	(Clifton and Motta, 1998)
	Halichoeres garnoti	Yellowhead wrasse	10	21	0.22	
	Halichoeres maculipinna	Clown wrasse	11	18	0.30	
	Lachnolaimus maximum	Hogfish	290	209	1.07	
	Thalassoma	Bluehead	5	7	0.20	

	bifasciatusm	wrasse				
	Squalus acanthias	Spiny dogfish	20	501	-0.32	(Huber and Motta, 2004)
	Hydrolagus colliei	White-spotted ratfish	87	870	0.18	(Huber et al., 2004)
	Heterodontus francisci	Horn shark	206	2,948	0.23	(Huber et al., 2005)
	Chilomyceterus schoepfi	Striped burrfish	380	180	1.23	(Korff and Wainwright, 2004)
	Carcharhinus limbatus	Blacktip shark	32	1,274	-0.36	(Weggelaar et al., 2004)*
			423	22,092	0.01	

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